1996

Male Reproductive Success And The Mating System Of Bushy-tailed Woodrats

Michael Graham Topping

MALE REPRODUCTIVE SUCCESS AND THE MATING SYSTEM OF BUSHY-TAILED WOODRATS.

by

MICHAEL G. TOPPING

Department of Zoology

Submitted in partial fulfilment
of the requirements for the degree of
Doctor of Philosophy

Faculty of Graduate Studies
The University of Western Ontario
London, Ontario
July 1996

ISBN 0-612-15086-0

ABSTRACT

Bushy-tailed woodrats are nocturnal cricetid rodents distributed throughout the mountainous regions of western North America. Despite a number of studies on the population ecology of this species, little is known about the behaviour of males during the breeding season.

I investigated the reproductive behaviour of male bushy-tailed woodrats in three ways. First, I examined the spatial distribution of individuals within a breeding population, using radiotelemetry and mark-recapture livetrapping. Both males and females exhibited considerable overlap with animals of both sexes, and mean intersexual and intrasexual overlap values for each sex did not differ in two of the three years of study. This pattern of overlap is more indicative of a promiscuous mating system, than of harem polygyny, which had previously been suggested for this species.

Second, I examined the pattern of reproductive success among breeding males, using DNA fingerprinting to determine paternity of all juveniles. No multiple paternity within litters was observed in all years of study. Male woodrats appeared to gain matings by sequestering females throughout estrus, but were unable to restrict access to more than one female at a time. The distribution of male reproductive success, coupled with the spatial overlap of the population, suggests that bushy-tailed woodrats exhibit a roving-male promiscuous mating system.

Third, I investigated the manner in which male woodrats compete for access to females. I examined the relationship between male reproductive success and male characteristics that would be favoured under differing mechanisms of male intrasexual competition. Traits associated

with scramble, reproductive endurance, and contest competition showed no significant correlations with reproductive success. However, traits associated with choice by females and sperm competition showed significant correlations with male reproductive success.

I conclude that woodrats exhibit a promiscuous mating system where males attempt to sequester females to ensure paternity of the litters. This male mating strategy is most likely favoured in woodrats due to the short, asynchronous, periods of estrus, and the large, unpredictable, movements of females.

Keywords: Bushy-tailed woodrat, *Neotoma*, radiotelemetry, DNA fingerprinting, mating system, male reproductive success, paternity.

Acknowledgments

The collection of the field data for this thesis would not have been possible without the stalwart efforts of Jean-Philippe (Git) Bechtold, Nicole (Wood Nymph) Swerhun and James (Hurlehey Boy) Goddard, who held the dubious honour of working alongside me during the course of this study. Despite the early mornings and late nights that this study required, they were always there, and as enthusiastic as anyone can be in the early hours of the morning. Thanks guys, I couldn't have done it without you. The staff of the University of Calgary Kananaskis Field Station always seemed to be there whenever I needed them. For the solving of various problems, their overall patience, and coffee break entertainment, I thank Grace, Judy, Ed, Mary and Ernst. Particular thanks to Ed Behr for his friendship and help in my 3 years at Kananaskis. My time in the field was also made easier by the help of several members of the mousecrew and other researchers at the station who shared the experience of moonlight telemetry. Special thanks to my mentor- Taye Teferi, the Rastaman, who showed me that there's no problem in the field that can't be solved by hard work, a sense of humour, and a cold Kokanee. Cheers, buddy!

My first meeting with my supervisor, Jack Millar, was reminiscent of the first meeting between Luke and Yoda, except that he didn't cook for me. As I got to experience Jack both in the field, and at Western, I realized that like the mighty Jedi master. there was much that I could learn from him, and that he was equally likely to provide a gem of wisdom or drop me on my head. His support and advice have always been given without question, and I am deeply indebted to him for all that he has passed on to me. Thanks Boss.

My time in the Molecular Ecology Unit (where the real work is done) of the Zoology department were made possible by two people. Shiva Singh provided me with space "upstairs", and cheerfully tolerated the fact that an ecologist was running loose in his lab. Dave Ribble (Molecular Ecologist bar none) patiently took me under his wing and introduced me to the wonderful world of DNA fingerprinting. Even though Dave didn't see the final results, I often was inspired by the thought of him laughing uproariously as I made yet another blunder in this strange field of science.

The advice offered and patience shown by the more permanent members of Shiva's lab was much appreciated, and for that, I thank Rebecca Ott, Andor Kiss, Indira Pillay, Kathleen Hill and Dody Reimer.

One of the first things that I realized at Western was that the smooth running of the Department was truly something to experience. For always being there when I needed answers, official letters, stamps or a kick in the pants, I would like to thank Mary, Jane, Melina and Sherri. My time in the Zoology department was made much easier by their hard work, and I am extremely grateful for all that they did for me. I would also like to take this opportunity to thank Ian Craig, for his seemingly endless good humour, and for making conference and departmental presentations look so good that any flaws in the data were overlooked.

Over the 5 years that I called Collip home, I was kept amused, well oiled and often distracted by a number of individuals, some of whom I can't seem to escape from. For various grad club, Filosophical and assorted gathering hangovers and good times, I blame Dave, Drew, Pam, Brian, Bee, Joe, Monika, Lee, Spence, Mike, Al, Shannon, Matina, Andrew, Neala, Paul, Tim, Fernando, Taye, Dave, Rich, Andor, and anyone else I may have missed. A grateful thanks to all my fellow 112ers, who maintained an extremely work-conducive atmosphere over the years.

The final format, and content of this thesis have been greatly improved thanks to the critical evaluation of a number of people. Thanks to the mousecrew past and present for always spotting the things that I missed, or explaining the things that I just didn't get. Dave Ribble, Rich Moses, Taye Teferi, Duncan Innes, and of course Jack introduced me to the wonderful world of small mammals, and various offerings at mouse meetings have been markedly improved by the sharp minds of Monika Havelka, Ann Hubbs, Matina Kalcounis, Neala MacDonald, Andrew McAdam, Bonnie Woolfenden, and various 4th year types. Thanks also to Gary Umphrey who greatly improved on my attempts at statistical modeling.

No thesis would be complete without the final hurdle of the defense, and I would like to thank my examining committee of Bob Bailey, Paul Cavers, Greg Kelly and Nancy Solomon for their unique blend of challenging questions, insightful revisions, and Spinal Tap references during my 2 hours in the hot seat. I would like to acknowledge the efforts

of Paul Handford who reviewed the entire thesis prior to submission, and who harangued me only slightly regarding the lack of papers on "really interesting organisms" in my reference section. Thanks also to Terence Laverty for serving on my advisory committee during the course of my degree.

Financial support for this thesis was provided by the award of a Commonwealth Scholarship, through the Commonwealth Scholarship and Fellowship Plan. I am extremely honoured and deeply grateful to be the recipient of such a prestigious award. Additional funding was provided by a National Science and Research Councils of Canada award to Jack Millar, and also by a Special University Scholarship from the University of Western Ontario. The undertaking and completion of this thesis would have been impossible with such generous support- thank you all.

As is seemingly traditional for the last paragraph, I would like to thank my family, for their years of love and encouragement. There aren't many people who still believe that you're capable of much when you're scoring 26% on 2nd year University midterms, and I know that I would never have made it this far without the support of my parents, sister, and extended family. Finally, I would like to thank Margo- my rock and my life, who put up with my annual departure for the Rockies, and never once doubted that I'd be writing the acknowledgments for my thesis one day, even when I did.

Dedication

This thesis is dedicated to all my school teachers and university lecturers who made the whole process of learning both challenging and enjoyable. For your enthusiasm, expertise, patience, and everything that I ever learned, this thesis is gratefully dedicated.

"Try not. Do, or do not. There is no try". - Yoda.

5th May 1992

"So, how were the rats, Mike?"

"Oh, not too bad, Jack."

"What condition were they in?"

"Um, I dunno. Pretty good, I think- they looked healthy."

"No, I mean, what condition reproductively?"

"Ohhhhh....."

TABLE OF CONTENTS

CERTIFICATE OF EXAMINATION / ii
ABSTRACT / iii
ACKNOWLEDGMENTS / v
DEDICATION / viii
TABLE OF CONTENTS / ix
LIST OF TABLES / xi
LIST OF FIGURES / xii

CHAPTER 1. GENERAL INTRODUCTION. / 1

CHAPTER 2. GENERAL METHODS. / 8

2.1 Study Area / 8
2.2 Demographic Information from Livetrapping / 9
2.3 Litter size and Maternity of litters / 11

CHAPTER 3. HOME RANGE SIZE AND SPATIAL DISTRIBUTION. / 13

3.1 Introduction / 13
3.2 Methods / 17
3.2.1 Radio Collars / 17
3.2.2 Calibration of Receiver / 17
3.2.3 Radio Telemetry and collection of positional data / 18
3.2.4 Home Range Analysis / 20
3.2.5 Overlap Analysis / 21
3.3 Results / 23
3.3.1 Radio Collars / 23
3.3.2 Calibration of Receiver / 23
3.3.3 Positional data / 24
3.3.4 Home Range Size / 24
3.3.5 Spatial Distribution / 25
3.4 Discussion / 27

CHAPTER 4. PATERNITY OF LITTERS AND THE MATING SYSTEM. / 38

4.1 Introduction / 38
4.2 Methods / 44
4.2.1 Extraction, restriction and Southern Transfer of DNA samples / 44
4.2.2 RNA Hybridization of DNA / 44
4.2.3 Scoring of DNA fingerprints / 45
4.2.4 Paternity Identification / 46
4.3 Results / 48
4.3.1 Litter size and maternity / 48
4.3.2 DNA fingerprinting and paternity identification / 49
4.3.3 Characteristics of the mating system / 49
4.4 Discussion / 51

CHAPTER 5. MALE REPRODUCTIVE SUCCESS AND INTRASEXUAL COMPETITION. / 68

5.1 Introduction / 68
5.2 Methods / 72
5.2.1 Male Reproductive Success / 72
5.2.2 Mechanisms of Male Intrasexual Competition / 72
5.3 Results / 75
5.3.1 Male Reproductive Success / 75
5.3.2 Mechanisms of Male Intrasexual Competition / 75
5.4 Discussion / 77

CHAPTER 6. GENERAL CONCLUSIONS. / 85

LITERATURE CITED / 88
VITA / 102

LIST OF TABLES

Table	Description	Page
Chapter 3.		
1	Population density on each outcrop (1992-94).	30
2	Receiver calibration data for each telemetry station.	31
3	Home range sizes of males and females.	32
4	Mean number of same and opposite sex neighbours overlapped by males and females.	33
5	Mean overlap index values for males and females.	34
Chapter 4.		
6	Distribution of litter sizes.	58
7	Gel scoring data from DNA fingerprints.	59
8	Parental table for all successful litters in 1992.	60
9	Parental table for all successful litters in 1993.	61
10	Parental table for all successful litters in 1994.	62
11	Estrus periods preceding successful litters in 1992.	63
12	Estrus periods preceding successful litters in 1993.	64
13	Estrus periods preceding successful litters in 1994.	65
Chapter 5.		
14	Mean, SD and ranges of male characteristics associated with male intrasexual competition.	80

LIST OF FIGURES

Figure	Description	Page
Chapter 2.		
1	Diagram of study area showing relative sizes and positions of the 4 outcrops.	12
Chapter 3.		
2	Minimum convex polygon home ranges for (a) males and (b) females in 1992.	35
3	Minimum convex polygon home ranges for (a) males and (b) females in 1993.	36
4	Minimum convex polygon home ranges for (a) males and (b) females in 1994.	37
Chapter 4.		
5	Reproductive success distributions for males and females in (a) 1992, (b) 1993, and (c) 1994.	66
6	Probability of detecting multiple paternity with varying percentage of litters involving 2 males mating with a female.	67
Chapter 5.		
7	Distribution of male reproductive success over the period of study.	81
8	Correlation between male reproductive success and the number of mates.	82
9	Correlation between male reproductive success and growth rate.	83
10	Correlation between male reproductive success and the number of male nest sites within a 100m radius.	84

CHAPTER 1.

GENERAL INTRODUCTION.

The different reproductive strategies of males and females have often been attributed to differences in the degree of parental investment exhibited by each sex. Trivers (1972) defined parental investment as "any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproducing) at the cost of the parent's ability to invest in other offspring." Subsequent research suggested that the sex that contributed less parental investment was generally free to pursue additional matings, and therefore would compete for mating access to the opposite sex. Accordingly, the sex that invests more appeared to be more 'choosy' in terms of mate selection (Bateman 1948; Orians 1969; Trivers 1972). However, more recent investigations have suggested that appropriate tests of this theory have not been performed, because we have limited information on the costs associated with reproduction in both sexes (Bailey 1992; Clutton-Brock and Parker 1992). Males may certainly contribute less energetically in terms of gametes and direct parental investment, but may more than make up for this in other ways, such as decreased survival through aggressive intrasexual competition (Clutton-Brock et al. 1982; Anderson and Fedak 1985; Deutsch et al. 1990), or a higher probability of predation due to mate-searching tactics (Svensson 1988; Kruuk 1995). In addition, several examples have been documented where the sex that invests less is not necessarily the predominant competitor for mates (Kluge 1981; Wootton 1984; Svensson 1988).

Clutton-Brock and Parker (1992) demonstrated that mate competition may be strongly influenced by biases in the operational sex ratio (the ratio of reproductively active males and females at a given time), where the sex that has more individuals ready to breed at a given time will compete for access to the opposite sex.

Until more empirical studies that catalogue and evaluate the relative costs of reproduction for males and females are conducted, it is perhaps wise to consider competition for mates as not arising from a single factor (operational sex ratio, parental investment, mate accessibility), but more as the result of a combination of such factors. The effect of these factors determines the mating system, or the combination of behavioural strategies employed by each sex to obtain matings (Emlen and Oring 1977). A number of theoretical descriptions of the four major mating systems have been documented, and can be summarized as follows (Orians 1969; Emlen and Oring 1977; Wittenberger 1979; Handford and Mares 1985).

A monogamous mating system typically involves a situation where there are equal numbers of males and females, where females reproduce in synchrony, and biparental care is required to successfully raise offspring (Emlen and Oring 1977; Kleiman 1977; Wittenberger 1979). In such a system, neither sex benefits by deserting their partner and attempting to gain additional matings, because (i) they are unlikely to find an unmated member of the opposite sex, given the 1:1 sex ratio, (ii) all individuals are engaged in the nurturing and rearing of their own offspring, and (iii) their offspring are increasingly unlikely to survive, because only one parent is raising them (Ribble 1992). If monogamy represents one extreme, the other is a promiscuous system, where neither, or only one parent is required to successfully raise the offspring. Reproduction may be

asynchronous and the population or operational sex ratio may be biased (Emlen and Oring 1977; Wittenberger 1979). In such situations, both sexes are free to pursue additional matings, both within or between periods of sexual receptivity and, due to the lack of a pair bond and the responsibilities of shared parentage, both sexes are capable of multiple matings without detrimental effects to their offspring. Somewhere along this continuum of monogamy to promiscuity (depending on the variables under consideration) lie the remaining two mating systems; polygyny and polyandry (Emlen and Oring 1977; Wittenberger 1979). Both of these mating systems are usually categorized by uniparental care, a biased operational sex ratio, and the ability of the competing sex to control access or mating rights to multiple members of the opposite sex (polygyny: males control access to females, polyandry: females control access to males). Such mating systems may involve a high cost of reproduction for the competing sex, due to the resources allocated to defense of the opposite sex.

The factors that influence and determine mammalian mating systems were reviewed by Clutton-Brock (1989), who suggested that the majority of the variation among mammals in male mating behaviour (i.e., the strategies employed in a promiscuous, polygynous or monogamous mating system) can be explained by the potential for males to defend access to females. If females live in close groups, where they either share a common home range, or have small, overlapping home ranges, there is a high potential for males to defend a range that encompasses the entire area of activity of all females. In such situations, one or two males may be able to defend access to the females, and claim exclusive mating rights (Schaller 1971; Rood 1986; Nishida and Hiraiwa-Hasegawa 1987). In contrast, if

females do not live in stable groups, or have large, undefendable areas of activity, then the behaviour of males must differ, since they would be unable to control access to females (Gosling 1986; Clutton-Brock et al. 1988). From the studies conducted to date, it appears that in general, the behaviour of males is very much affected and determined by the behaviour of females (Clutton-Brock 1989). Therefore, to understand the environmental pressures that determine males' reproductive behaviour (Clutton-Brock 1989), we must consider the manner by which males obtain matings, and the factors influencing the relative success of individuals. The purpose of this thesis is to examine the factors that determine reproductive behaviour of male bushy-tailed woodrats *(Neotoma cinerea)*.

The bushy-tailed woodrat is the largest and most northerly-living species of the genus *Neotoma*, distributed from the southern Yukon to northern New Mexico, generally following the Rocky Mountains (Burt and Grossenheider 1976). It is a nocturnal, non-hibernating herbivore, feeding on a variety of plant material (Finley 1958; 1990). Local distributions of *N. cinerea* are limited by the availability of suitable den sites, located in fissures within rocky outcrops, caves, or rockpiles (Finley 1958; Escherich 1981; Hickling 1987). Such den sites are vital to the survival of *N. cinerea*, particularly in more northern climates, for thermoregulatory reasons (Vaughan 1990). The large rock bluffs act as heat sinks during the winter, allowing *N. cinerea* to maintain an ambient temperature within the nest that may be 10 - 15 °C higher than the outside air temperature (Brown 1968). In the summer, the rocks act as buffers against high temperatures (Brown 1968). However, reliance on such den sites may dictate that other resources (e.g., food) are located at some distance from the nest. *N. cinerea* den in the rocks, but venture into the surrounding forest at night to

forage (Escherich 1981). In common with the majority of *Neotoma* species, *N. cinerea* caches plant material within its permanent den site (Finley 1958; 1990). Such caches are capable of supporting the energetic demands of woodrats for up to 3 days, but can only support the demands of a lactating female for less than a day (Hickling et al. 1991).

Reproduction is highly seasonal in *N. cinerea* (February - August), particularly in the northerly parts of its range, where breeding usually takes place from late April to mid August (Egoscue 1962; Escherich 1981). Females produce one or two (occasionally three) litters per season, consisting of 3 - 5 pups at birth, and 0 - 3 at weaning (Hickling 1987; Moses 1992). Gestation lasts approximately 30 days, and is followed by a lactation period of at least 3 weeks (Egoscue 1962; Escherich 1981). Neither sex becomes reproductively active during the season after birth (Moses 1992). Dispersal is male-biased in *N. cinerea*, with juvenile females often establishing themselves in close proximity to their mothers. This behaviour confers an advantage to juvenile females in the form of enhanced survival and lifetime reproductive success (Moses 1992). This aggregated distribution of females within outcrops, coupled with (i) the trend for operational sex ratios within an outcrop to be male biased, (ii) the largest degree of sexual dimorphism within the genus *Neotoma*, and (iii) a high environmental potential for polygyny, in that females are aggregated on outcrops, and exhibit asynchronous estrus, have led to suggestions that the mating system exhibited by *N. cinerea* is harem-defense polygyny, or promiscuity (Finley 1958; Escherich 1981; Hickling 1987).

Despite the number of population studies on *N. cinerea*, and the numerous suggestions regarding male reproductive behaviour and the mating system, the behaviour of males during the breeding season is not

well documented. Escherich (1981) and Moses (1992) both report that males have larger home ranges that females, and that while the areas of female activity overlap considerably, males do not appear to exhibit the same degree of spatial interactions. Such a spatial distribution appears to support the predictions of a polygynous mating system. As the result of a large-scale livetrapping investigation into the group dynamics of *N. cinerea*, Hickling (1987) suggested that males may exhibit one of three different mating strategies during the breeding season, with approximately half of the males (54%) remaining on a single outcrop and attempting to mate with the resident females on the same outcrop. The remaining males were divided evenly between those individuals that were resident over a study area, but roamed between outcrops, and those that moved between study areas, which were classed as non-territorial transients (Hickling 1987). Similar variations in apparent mating strategies (resident vs. roamers, or dominant vs. sneakers) have been observed in other mammals (Le Boeuf 1974; Clutton-Brock et al. 1982), insects (Alcock et al. 1977), fish (Gross 1985) and amphibians (Howard 1978).

The goal of this thesis is to investigate the reproductive ecology and behaviour of male bushy-tailed woodrats by quantifying the various characteristics of males that may affect the patterns of reproductive success (Clutton-Brock 1988) and genetic fitness of each individual. By examining the mating strategies employed by each male, and the resulting relative fitness, it will be possible to evaluate the relative importance of ecological, morphological and behavioural factors in determining male reproductive behaviour.

The information in this thesis is divided into 5 chapters. Chapter 2 outlines the study area, and the methodology used throughout this study.

Chapter 3 describes the spatial distribution of woodrats, based on movements within the rocky outcrop habitat and the surrounding forest habitat. In Chapter 4, I examine the reproductive success of males within the population, using DNA fingerprinting to assign paternity of juveniles with known maternity. Finally, in Chapter 5, I investigate the mechanism of male intrasexual competition within *N. cinerea* by determining which behavioural and morphological traits of male woodrats show significant relationships with reproductive success.

CHAPTER 2.

GENERAL METHODS.

2.1 Study Area.

Field work was carried out in the Kananaskis Valley, southwestern Alberta (51° N, 115° W), from late April to the end of August over a three year period (1992 - 94). The study area consisted of 4 rocky outcrops ranging from 170 - 300 m in length (Figure 1) and located on the east facing slope of three adjacent hills along Highway 68 (Sibbald Creek Trail). These outcrops (total area: 30 ha) had previously been used in population studies of woodrats (Hickling, 1987; Moses 1992), and were chosen because they allowed an adequate number of individuals (25 - 35) to be monitored within a single study area. The next suitable woodrat habitat was located approximately 750m away.

The vegetation in the study area is typical of subalpine habitats (Ogilvie 1969). All outcrops were located at 1670 metres above sea level (m.a.s.l.), and were surrounded by mature mixed coniferous (White spruce, *Picea glauca*, Douglas Fir, *Pseudotsuga menziesii*, and Lodgepole pine, *Pinus contorta*) forest with a mixed shrub understory (Bearberry, *Arctostaphylos uva-ursi*, Common juniper, *Juniperus communis*, Buffaloberry, *Shepherdia canadensis*, and *Ribes* spp.). Small mammals commonly encountered on the study area included red squirrels *(Tamiasciurus hudsonicus)*, chipmunks *(Eutamias* spp.*)*, Northern flying squirrels *(Glaucomys sabrinus)*, golden mantled ground squirrels *(Citellus*

lateralis), deer mice *(Peromyscus maniculatus)* and long tailed voles *(Microtus longicaudus)*. Potential predators of woodrats (Great Horned owls, *Bubo virginianus*, Marten, *Martes americana* and coyotes, *Canis latrans*) were also recorded throughout the study area.

2.2 Demographic Information from Livetrapping.

In order to gather information about the relative locations of the outcrops and trapping stations, I first mapped the study area by placing permanent markers at 25 m intervals across the three hills. Seven lines, running E-W across the hills and separated by 50 m were established. The entire study area (1000 m x 300 m) was marked in this way. Positions of trap stations, and locations of nests could then be calculated by triangulating from 2 or more permanent markers.

Livetrapping was conducted on each outcrop once per week, using Tomahawk model 201 traps. Due to the nature of the habitat, and because information on all resident individuals was required, the traps were arranged non-randomly along the base of each outcrop, in areas of obvious woodrat activity as indicated by fresh urine, faeces or nest sites. Between 17 and 35 traps were set on each outcrop, depending on the length and the number of resident animals. Traps were set at night, baited with peanut butter and a slice of apple, and checked the following morning, between 0630 and 0830. When not in use, traps were collapsed and left at the trap station.

When a woodrat was caught, it was transferred from the trap to a pillowcase, and weighed using a 1000 g Pesola spring scale. The woodrat was then removed from the pillowcase, and eartagged (Monel #1005) at

initial capture. A small sample of tissue was also taken from each ear of every animal for genetic analysis. Tissue samples were placed in a 1.5 ml cryovial, which was transferred to a small cooler containing an ice pack to ensure that the tissue sample did not degrade before it could be stored in a -70° C freezer at the field station. Three linear measures were then recorded; head length (tip of nose to back of skull), body length (tip of nose to base of tail) and tail length (tip to base). The age of the animal was then assessed as either a juvenile (born that year), yearling (born the previous year) or adult (at least 2 years old). Juveniles were identified by their relatively smaller body size, and grey pelage, in contrast to the brown pelage of adults and yearlings. Yearlings were distinguished from adults based either on previous trapping records, or by weight. From weights of animals of known age at first capture, yearlings were identified as those animals weighing ≤340 g for males, and ≤285 g for non pregnant females. Male reproductive condition was assessed as either scrotal or abdominal testes. Females with perforate vaginas were considered to be undergoing estrus, and reproductive status was recorded as pregnant, lactating, pregnant and lactating, or post-reproductive. Animals were considered residents if they were captured on a minimum of 3 occasions in 4 successive trapping sessions, and persisted on the grid for ≥2 months. Overwintered animals that had previously been classed as residents were automatically defined as residents in the following year, because animals in breeding condition rarely move from the area in which they first become established (Moses 1992).

2.3 Litter size and Maternity of litters.

Litter sizes of all resident females were calculated as the number of offspring that emerged from the natal nest at weaning. Juveniles are usually not captured until around 15 days of age, which is approximately the start of weaning (Moses 1992). When a juvenile was captured on the study area, I first assessed whether the juvenile had been born on the outcrop that it was captured on. Moses (1992) employed radioisotopes to unambiguously determine maternity of juveniles (Tamarin et al. 1983), and gathered data on juvenile weight at first capture in relation to the location of the mother's nest. He found that in approximately 95% of cases, a juvenile had been born on the outcrop on which it was captured if it weighed ≤180 g for males, and ≤160g for females (R. Moses, per. comm.). Therefore, I used these criteria to identify the natal outcrop of each juvenile. If juveniles weighed more than these values at first capture, I assumed that they had not been born on the study area. Given that the natal outcrop of the juvenile could be identified, I then assessed maternity, based on (i) the location of capture relative to the nests of resident females on the outcrop, and (ii) the estimated date of birth, based on the weight of the young (Moses 1992), compared to the reproductive history of each resident female. Due to the asynchrony of estrus in female woodrats (Egoscue 1962), there was usually only one female that could have given birth to a particular juvenile. If maternity was uncertain, or could not be assessed from demographic data, I assigned maternity based on genetic analysis.

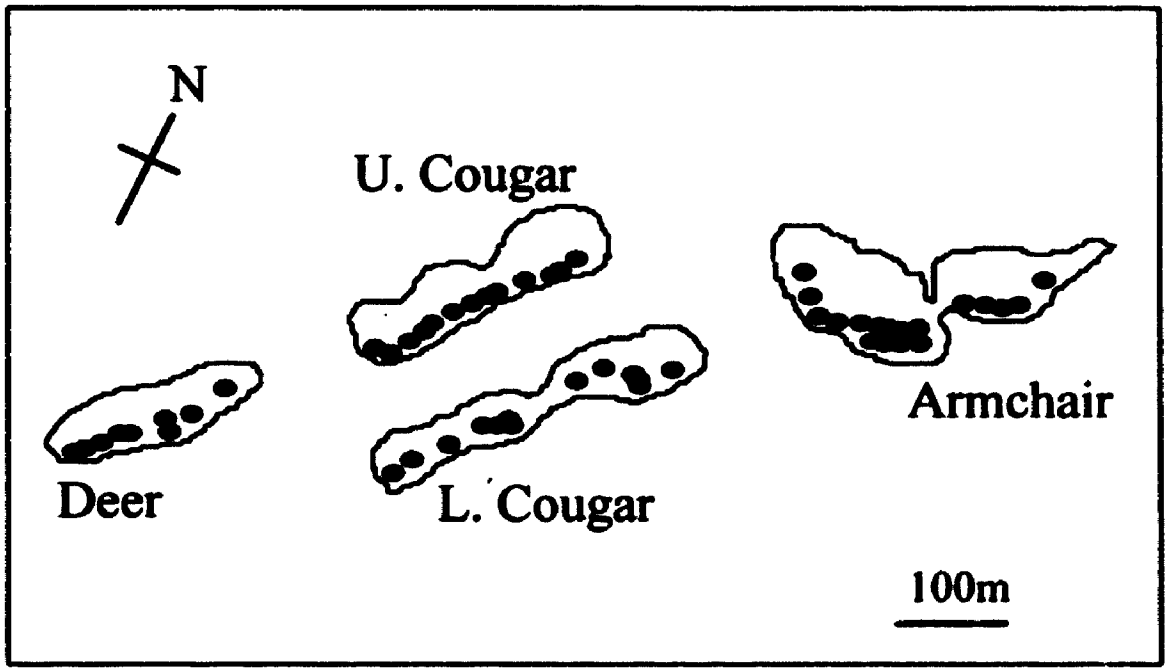

Figure 1. Relative sizes and locations of the 4 outcrops used in this study (total area 30 ha). Trap sites are shown as black circles.

CHAPTER 3.

HOME RANGE SIZE AND SPATIAL DISTRIBUTION.

3.1 INTRODUCTION

Spatial distribution and presumed interactions of individuals have been studied by home range analysis for a variety of mammalian species (e.g., Cranford 1977; Kruuk 1978; Ostfeld 1986; Ryser 1992). The home range is defined as "a more or less restricted area within which an animal moves when performing its normal activities" (Burt 1943). Various methods can be used to calculate the home range size (minimum convex polygon, Southwood 1966; probability ellipse, Van Winkle 1975; cluster analysis, Kenward 1987; and isopleths centered on the harmonic mean of the range, Dixon and Chapman 1980), but all define a boundary around the area within which an animal moves.

Home range analysis has been used to provide a general classification of mating systems by documenting two parameters; the relative size of male and female home ranges and the degree to which the home ranges of each sex overlap with members of the same, and the opposite sex (Cameron and Spencer 1985; Salvioni 1988; Cantoni and Vogel 1989; Ribble and Salvioni 1990). For mammals in general, the home range size of females is thought to be influenced by energetic demands, and to be related to the availability of food (Ostfeld 1985; Clutton-Brock 1989). In contrast, male home range is generally thought to be affected more by the spatial distribution of females, and their economic defensibility (Trivers

1972; Emlen and Oring 1977; Ims 1987) than by food. The extent to which females are aggregated into non-territorial groups, or separated into small, adjacent areas of occupied space, defines the environmental potential for polygyny (EPP), or the potential for a single male to monopolize a group of females (Emlen and Oring 1977). In order to gain exclusive access to more than one female, a male must occupy an area that is large enough to include the home ranges of more than one female (Madison 1980; Ostfeld 1986). In contrast, similarly sized male and female home ranges are usually indicative of a monogamous mating system (Getz and Hoffman 1986; Ribble and Salvioni 1990). Male and female home range sizes can therefore be used as proximate indicators of the mating system (Gaulin and Fitzgerald 1988; Salvioni 1988). If the home range size of a male is larger then that of a female, males are presumably attempting to encounter and mate with more than one female (Lambin et al. 1992). Therefore, determination of the relative sizes of male and female home ranges provides indirect information regarding the mating system and social organization. Such data provides a general index of the mating system (e.g., polygyny, promiscuity), without being able to classify the type of mating system further (e.g., harem polygyny, hierarchical promiscuity). In addition, variation in home range sizes within sexes has also been used as indicators of the mating system. Variation in male home range size (especially when males of a particular age have smaller home ranges) may be indicative of differing male reproductive strategies, e.g., in a harem polygynous system, dominant males have smaller home ranges than subordinate males, which roam from harem to harem, attempting to gain matings (Le Boeuf 1974; Clutton-Brock et al. 1982; Davis and Murie 1985).

Although the relative home range size of each sex may function as an indicator of the mating system, the ability to define mating systems from these data is limited, because they provide no information regarding the spatial distribution of the population. For example, male home ranges are larger than those of females in both promiscuous and polygynous systems, but only polygynous males exhibit territoriality. Therefore, more recent investigations into the link between home range sizes and mating systems have focused on the degree of home range overlap with animals of the same sex (intrasexual overlap), and the opposite sex (intersexual overlap) (Ostfeld et al. 1988; Lambin and Krebs 1991; Boellstorff and Owings 1995). On the basis of previous studies of spatial distribution and mating systems, the following predictions can be made. In a monogamous system, male-female pairs occupy an exclusive area. As a result, they are unlikely to interact with other conspecifics, and both sexes will show greater intersexual than intrasexual overlap (Hofmann et al. 1984; Getz and Hofmann 1986; Ribble and Salvioni 1990). Polygyny is characterized by dominant males controlling access to females (Emlen and Oring 1977; Wittenberger 1979). As such, male-male overlap is low, in comparison to the high level of male-female overlap resulting from defense of females. In contrast, female-female overlap will be high, compared to female-male overlap (Ostfeld et al. 1985). Polyandry, where females control access to males shows a similar pattern to polygyny, except the roles of the sexes are reversed (Emlen and Oring 1977; Wittenberger 1979). As such, a polyandrous system is characterized by low female-female and male-female overlap, compared to high levels of male-male and female-male overlap. A promiscuous system exists when each sex has access to multiple mates (Emlen and Oring 1977; Wittenberger 1979). Males show relatively similar

levels of intersexual and intrasexual overlap, while females exhibit either equivalent levels of intersexual and intrasexual overlap, or higher intersexual than intrasexual overlap, depending on the degree of female territoriality (Ostfeld 1985).

The spatial distribution of bushy-tailed woodrats has previously been investigated, but only in a limited fashion. Moses (1992) documented linear overlap along the outcrops between adult and yearling females, and concluded that overlap between home ranges is often large. In addition, males had longer home ranges than females within the outcrop (Moses 1992). Although this provided valuable information on the spatial distribution within outcrops, no measures within the forest habitat were attempted. An earlier study using radiotelemetry on a small number of individuals in California (Escherich 1981) documented that the home ranges of bushy-tailed woodrats overlapped considerably, and it appeared that males were territorial, indicating polygyny. However, no quantitative analysis was performed by Escherich (1981), so the degree of intersexual and intrasexual overlap of each sex was not evaluated.

Given that bushy-tailed woodrats utilize rocky outcrops for nest sites, and the surrounding forest for food, any investigation into the spatial distribution of these animals should consider activity in both habitats. There were two objectives to this study. First, the home range size of individuals within the population was measured, in order to describe and quantify areas of activity. Secondly, the degree of interaction between individuals (overlap between areas of activity) was determined, in order to describe the level of intersexual and intrasexual overlap for both sexes.

3.2 METHODS

3.2.1 Radio Collars.

Radio collars (Model No. PD - 2C, Holohil Systems Ltd., Ontario, Canada.) were fitted to resident, reproductively active animals in all years. In order to fit radiocollars, animals were lightly anaesthetized using Metofane® by placing 4 - 7 drops on cotton wool in the bottom of a small (100 ml) glass jar, and placing the woodrats' head inside the opening of the jar. The time taken for anesthesia varied with each individual, and ranged from 30 seconds to 3 minutes. Once anaesthetized, the circumference of the animals' neck was measured, and a length of rubber tubing (2 mm diameter) cut to length. The tubing slid over the antenna wire of the collar, to ensure that the wire did not cut into the neck. The radio collar was attached by crimping one or two small lengths of brass tubing to the antenna wire. Once the collar had been secured, and it was confirmed that it did not interfere with respiration, the woodrat was placed back in a trap, and left covered for at least 20 - 30 minutes to allow full recovery.

3.2.2. Calibration of Receiver.

Only one receiver was used for radio telemetry, and triangulation was therefore not an option. Therefore, I calibrated the receiver to obtain an estimate of distance. The receiver used in this study was a Lotek model SRX_400 (Lotek Engineering Inc., Ontario) fitted with a 3 tine Yagi-style antenna. In order to account for the variation in habitat structure between study sites, I calibrated the receiver for each telemetry station. A

radiocollar was tied to the boot of an assistant, to simulate the height that a woodrat would be off the ground. My assistant then walked down the hill, away from the receiver, stopping at 5 meter intervals. I would then obtain a value for signal strength from the receiver, as shown on the digital display. Readings were repeated at 5m intervals until no signal could be obtained. Calibration graphs comparing signal strengths with distance were then constructed.

3.2.3. Radio Telemetry and collection of positional data.

Due to the physical structure of the study sites, it was not possible to move towards a radiocollared animal once a signal had been located. Therefore, I employed a static method of radiotelemetry, utilizing telemetry stations of known and fixed position. I established 3 or 4 telemetry stations on each outcrop, depending on the outcrop length. Due to the relative difficulty in moving between outcrops at night, I performed telemetry on only one outcrop per night. A typical telemetry session would proceed as follows. I scanned the set of radio frequencies, and on locating a signal, attempted to determine the position of the woodrat by estimating the direction and distance from the telemetry station. Only signals that (a) gave a strong enough signal, as indicated by a signal strength of greater than 50 on the receiver display, (b) were clear signals, without any static or other distortion and (c) came from the surrounding forest, rather than the rocky outcrops were used. If a signal did not meet all three criteria, it was discarded from the analysis. If a signal was suitable, I recorded the signal strength, and the compass bearing from the station to the signal. In order to maximize the data set, I performed a scan of all frequencies at 10

minute intervals at the telemetry station. If the outcrop had 4 telemetry stations, I remained at each station for 50 minutes (5 scans) or 30 minutes (3 scans) if no signals were obtained. If there were 3 stations on the outcrop, I remained at each station for 70 minutes (7 scans) or 40 minutes (4 scans) if no signals were obtained. In 1992, I began scanning for radio signals as soon as it started to get dark, at approx. 2230 - 2300 hours. However, I found that woodrats did not become active until 2345 - 0000 hours, and remained active only until approx. 0400 hours, a maximum period of activity of 4 hours. Before and after this period of activity, radio signals were occasionally located, but were all traced to a known den site. Therefore, in 1993 and 1994, radio telemetry commenced at 2345 hours, and continued until 0400 hours, or until no signals were located in the surrounding forest.

The location of each radio signal was determined by first using the calibration graphs to estimate the distance between the telemetry station and the source of the signal. Then, the location was plotted on a scale (1:200) map of the area, using the compass bearing to give the direction from the station. A large grid was superimposed over the map, and all locations were converted to Cartesian coordinates. If more than one fix was gathered for an individual animal in a given night, I tested for independence of location, using the formula from Swihart and Slade (1985). Any dependent fixes were removed until all data points were independent. In addition to radio telemetry, positional data from live trapping was also used. Trap site locations were fixed for each breeding season, and the position of each trap was determined using the scale map of the study area.

I was concerned only with determining the spatial distribution as it relates to the mating system, so I used data only from the period where animals were reproductively active. I defined the breeding season as the period of time from the onset of sexual activity (males with scrotal testes and females entering estrus) to the cessation of sexual activity (males with abdominal testes and females having weaned their last litter of the season).

3.2.4. Home Range Analysis.

Home range calculations and overlap analysis were performed using the computer program RANGES IV (Kenward 1990). Before any home range analysis could be performed, it was necessary to determine the minimum number of independent locations required to accurately describe the home range of an individual. Using data from 1992 to plot an observation area curve, I determined that total home range size reached an asymptote when 14 fixes were collected. I therefore discarded any individual with fewer than 14 locations from subsequent analysis. Home range size was determined using the 100% minimum convex polygon method (Southwood 1966) which links all outer points to maximize the area described. In addition, this method results in more robust measures of home range size when a small number of fixes are used (Harris et al. 1990). Differences between home range sizes for each year and sex were calculated using General Linear Model (GLM) ANOVA. Significance was accepted at $p \leq 0.05$.

3.2.5. Overlap Analysis.

Overlap Indices (OI) were calculated for each pair of overlapping neighbours using the formula from Ostfeld (1986). The Overlap Index for a pair of animals x and y is as follows:

$$OIxy = 0.05(A/X_{0.95})(A/Y_{0.95}) + 0.5(B/X_{0.95})(B/Y_{0.5}) + 0.5(C/X_{0.5})(C/Y_{0.95}) + 0.95(D/X_{0.5})(D/Y_{0.5}).$$

Where: $X_{0.95}$ = 95% minimum convex polygon for individual x; $X_{0.5}$ = 50% minimum convex polygon for individual x; $Y_{0.95}$ = 95% minimum convex polygon for individual y; $Y_{0.5}$ = 50% minimum convex polygon for individual y; A = area of overlap between the 95% minimum convex polygons of x and y; B = area of overlap between the 95% minimum convex polygon of x and the 50% minimum convex polygon of y; C = area of overlap between the 50% minimum convex polygon of x and the 95% minimum convex polygon of y; D = area of overlap between the 50% minimum convex polygons of x and y. The index value generated by this equation ranges from 0 when ranges do not overlap, to 2.0 when two ranges are identical.

95% and 50% minimum convex polygons were calculated using RANGES IV, by excluding the appropriate fraction of fixes, located farthest from the harmonic mean (Dixon and Chapman 1980) i.e., 5% of fixes for 95% minimum convex polygons, and 50% of the fixes for 50% minimum convex polygons. The preceding formula was used because it places the most emphasis on overlap of the 50% minimum convex

polygons, which can be considered as the core areas of the animals' home ranges (Ostfeld 1986).

Cumulative Overlap Index ($\sum$OI) values were then calculated for each individual following Ostfeld et al. (1988) by summing the overlap with members of (i) the same sex, and (ii) the opposite sex. For the population as a whole, there were four categories of overlap; male-male, male-female (male overlapping with females), female-male (female overlapping with males) and female-female overlap. Each individual contributes overlap information to three of four categories; both intersexual overlap categories and its intrasexual overlap category. Values were square root transformed which resulted in normality and equal variance of data. Differences between overlap categories were analyzed by GLM ANOVA with the Tukey-Kramer test (Zar 1984). In addition, the relationship between the degree of intersexual and intrasexual overlap exhibited by individual animals was examined. By regressing log (intersexual overlap value) against log (intrasexual overlap value), the ratio of intersexual overlap : intrasexual overlap can be estimated as the slope of the regression line.

3.3 RESULTS

3.3.1. Radio Collars.

In 1992, 11 of 12 resident males, and 15 of 16 resident females received a collar, but radio collars were fitted to all resident, reproductively active animals in 1993 (8 males and 11 females) and 1994 (14 males and 9 females). The number of radio collars fitted to adults and yearlings of both sexes, separated by outcrop, is shown in Table 1. There was no mortality as the result of anesthesia, and all individuals that had a collar fitted were subsequently recaptured. Yearling male woodrats were the most affected by the radio collars, as they grew substantially during their second summer. Collars were routinely checked, and adjusted if too loose or tight. Overall, collars did not appear to alter the locomotory behaviour of woodrats.

3.3.2. Calibration of Receiver.

I plotted a calibration graph for each telemetry station used during this study. In all years, the maximum range of the radios was 70m. Graphs were plotted separately in 1992 and 1993, to control for any variation in receiver sensitivity following a minor repair to the receiver at the end of the 1992 field season. In 1994, a brief series of trials confirmed that the calibration graphs from 1993 were still accurate. Calibration graphs were linear in form, and error in distance estimation was calculated by plotting 95% confidence limits on the slope. Correlation coefficients and maximum error in determining the position of a radio signal for each telemetry station

are shown in Table 2. The maximum mean error in locating the source of a radio signal was < 5 m.

3.3.3. Positional data.

After removal of non-independent positional data, the mean number of locations per individual in each year was 22.2 (range 14 - 39) in 1992, 32.8 (range 14 - 74) in 1993, and 30.2 (range 15 - 72) in 1994. Including the positional data from live trapping increased the home range size in all cases, because live traps were located within, or adjacent to the rocky outcrops. The nest location was determined by daytime telemetry for each individual that was fitted with a radio collar. For all males and females, the nest site was contained within the boundaries of the home ranges.

3.3.4 Home Range Size.

Home range sizes were calculated for 5 males and 9 females in 1992, 8 males and 9 females in 1993, and 10 males and 8 females in 1994. The mean ($\pm$SE) values for home range sizes of each sex in all years are shown in Table 3. In all years, males had significantly larger home ranges than females ($F = 9.31$; $df = 1,43$; $p = 0.004$), but home ranges within each sex did not differ between years ($F = 2.14$; $df = 2,43$; $p = 0.130$) (Table 3). Male home range size was not correlated with weight while reproductively active ($r = -0.118$, $p = 0.593$), but showed an almost significant correlation with body length ($r = -0.46$, $p = 0.054$). There was no correlation with either body weight when non pregnant ($r = 0.013$, $p = 0.951$) or body length ($r = -0.207$, $p = 0.426$) for females. Home ranges

of both males and females overlapped considerably in all years (Figures 2 - 4). The mean number of neighbours overlapped (±SE) during the breeding period, for each overlap category and year are given in Table 4.

3.3.5. Spatial Distribution.

Cumulative overlap index values were calculated for 5 males and 9 females in 1992, 8 males and 9 females in 1993, and 10 males and 8 females in 1994. The two way ANOVA on overlap category and year showed a significant two way interaction ($F = 2.76$; $df = 6,86$; $p = 0.017$). As a result, comparisons were made among the four overlap categories for each year separately. Mean cumulative overlap index values (±SE) for all 4 overlap categories, by year are shown in Table 5. Comparisons between overlap values for each year were non-significant for 1992 ($F = 1.61$; $df = 3,24$; $p = 0.213$) and 1993 ($F = 0.38$; $df = 3,30$; $p = 0.770$). However, mean values differed significantly between overlap categories during 1994 ($F = 5.95$; $df = 3,32$; $p = 0.002$), as female-female overlap was significantly lower than all other overlap categories (Tukey-Kramer test).

There were no significant differences between intersexual and intrasexual overlap values for males during all years of study, and for females during 1992 and 1993 (Table 5). However, females showed significantly lower intrasexual overlap than intersexual overlap in 1994 (Table 5). To determine whether these findings were similar for each individual, the ratio of intersexual overlap to intrasexual overlap was calculated. By calculating the ratio, any differences due to differing magnitudes of overlap values between years were removed, and therefore,

data were pooled where appropriate. If individuals exhibited equal levels of intersexual and intrasexual overlap, the 95% confidence limits of the regression slope (representing the ratio of the two overlap values) should include the value 1.0. As males showed no difference between mean values of intersexual and intrasexual overlap for all three years, data were pooled for this period. The regression of log transformed data was significant ($t = 3.74$; $df = 21$; $p = 0.001$), with slope = 0.78, and a standard deviation = 0.21. The 95% confidence limits of the slope ranged from 0.37 - 1.19. As this range included 1.0, the degree of intrasexual overlap was considered equivalent to the degree of intersexual overlap for individual males in all three years. Females showed no difference between intersexual and intrasexual overlap for 1992 and 1993, so data for individuals from these years were pooled. The regression was significant ($t = 2.73$; $df = 14$; $p = 0.016$), with slope = 0.65 and standard deviation = 0.24. The 95% confidence interval for the slope of the regression ranged from 0.18 - 1.12, therefore it was concluded that individual females in 1992 and 1993 show a ratio of intersexual overlap to intrasexual overlap that did not differ from 1.0. In 1994, females showed a significant difference between intersexual and intrasexual overlap, where intersexual overlap was approximately double that of intrasexual overlap. In this case, the slope of the regression should include 2.0 within the 95% confidence interval. However, the regression was non significant ($t = 0.58$; $df = 6$; $p = 0.474$), although the slope was positive (0.38), indicating that females with high levels of intersexual overlap also showed relatively high levels of intrasexual overlap.

3.4 DISCUSSION

Males exhibited significantly larger home ranges than females in all 3 years. In addition, all males were trapped on outcrops other than the one where their nest was located, as opposed to females, which were only captured on the same outcrop as their nest. In contrast to Escherich (1981), there was no evidence for male territoriality, as indicated by the high degree of overlap between male home ranges in all years (Figures 2 - 4). Females also showed a high degree of overlap, indicating no territoriality. Overall, all animals of both sexes had home ranges that overlapped with at least 2 individuals of the opposite sex in all years (Table 4).

No significant differences were found between values for intrasexual and intersexual overlap for males in all years (Table 5). An equal degree of intersexual and intrasexual overlap was also exhibited by each individual male in all years of study. No significant differences were found between values of intersexual and intrasexual overlap for females in 1992 and 1993 (Table 5). Similarly, individual females exhibited an equal degree of intersexual and intrasexual overlap in 1992 and 1993. However, in 1994, females showed significantly lower intrasexual than intersexual overlap, both for the population as a whole (Table 5), and at an individual level. The significantly lower female-female overlap in 1994 appears to be the result of a less aggregated distribution of female nest sites than in either of the previous years (mean nearest neighbour distances; 48 m in 1992, 68 m in 1993, 113 m in 1994).

The degree of intrasexual overlap, relative to intersexual overlap, in females can be explained by considering two factors; (i) the kin association in this species, and (ii) the distribution of nest sites. Bushy-tailed woodrats

show close association between mothers and daughters, where daughters establish nest sites adjacent to their mothers (Moses and Millar 1992; 1994). Such behaviour allows daughters to experience enhanced survival and reproductive success when their mothers are present on the same outcrop (Moses and Millar 1992; 1994). This results in female woodrats exhibiting a mixed strategy towards female conspecifics, in that they are aggressive towards non-kin, but behave amicably towards kin (Moses and Millar 1994). Therefore, the degree of genetic relatedness in the population may affect the degree of female intrasexual overlap. When genetic relatedness is high, females will behave amicably towards kin, resulting in a higher degree of female intrasexual overlap. In addition, as suitable nest sites on rocky outcrops show clumped distribution and limited availability (Hickling 1987; Moses 1992), the area surrounding nest sites may not be economically defensible in years of high population density (Emlen and Oring 1977; Wittenberger 1979). Therefore, when the density of females is high, the degree of female intrasexual overlap may also be high. Variation in the degree of female intrasexual overlap is most likely due to a combination of female density and the degree of relatedness between females.

Previous research has suggested that bushy-tailed woodrats exhibit a polygynous mating system (Escherich 1981; Hickling 1987). In contrast to these earlier suggestions, my results show that there was no difference between male intersexual and intrasexual overlap, indicating promiscuity as the likely mating system. Females showed either no difference between intersexual and intrasexual overlap, or greater intersexual overlap, which is also consistent with the predictions of a promiscuous mating system. Further support for promiscuity can also be found in Table 4, which shows

that, on average, each sex overlaps with equal numbers of animals of the same and opposite sex.

Disagreement between these findings and previous research is most likely due to the fact that this study investigated movements of a large number of woodrats in both rocky outcrop and forest habitat. Previous studies have either investigated spatial distribution on rocky outcrops alone (Hickling 1987; Moses 1992), or have used radiotelemetry on a small number of individuals within a year (Escherich 1981). Although populations of bushy-tailed woodrats appear limited by the number of suitable nest sites on rocky outcrops (Finley 1958), there is little or no food available in this habitat. Investigation of movements in the forest surrounding the rocky outcrops revealed much larger areas of activity, coupled with a greater degree of overlap between individuals than previously suspected. These findings appear to be a more realistic representation of the spatial distribution of bushy-tailed woodrats than results of previous investigations. In conclusion, based on the spatial distribution alone, there is little support for a polygynous mating system, as the patterns observed are more indicative of a promiscuous system.

Table 1. Population sizes (defined as the number of resident animals) on each outcrop over the period of study (1992 - 94). The numbers of resident animals that were fitted with a radio collar are shown in parentheses.

Year	Sex/Age	Deer	U. Cougar	L. Cougar	Armchair
1	Adult Male	2 (1)	1 (1)	1 (1)	1 (1)
9	Adult Female	2 (2)	0	1 (1)	4 (4)
9	Yearling Male	0	1 (1)	3 (3)	3 (3)
2	Yearling Female	1(1)	2 (2)	2 (2)	4 (3)
1	Adult Male	0	1 (1)	2 (2)	2 (2)
9	Adult Female	1 (1)	0	1 (1)	5 (5)
9	Yearling Male	1 (1)	0	2 (2)	0
3	Yearling Female	1(1)	2 (2)	1 (1)	0
1	Adult Male	3 (3)	1 (1)	1 (1)	2 (2)
9	Adult Female	2 (2)	0	1 (1)	1 (1)
9	Yearling Male	0	2 (2)	3 (3)	2 (2)
4	Yearling Female	0	3 (3)	2 (2)	0

Table 2. Pearson product-moment correlation statistics for telemetry receiver calibration graphs. Correlation coefficient (r) and maximum error in locating source of signal (from 95% confidence intervals of the slope) are shown for each telemetry station for 1992 and 1993. Calibration graphs from 1993 were used for the 1994 data.

Station	1992			1993		
	r	p	Error	r	p	Error
A1	-0.972	0.001	±5m	-0.915	<0.001	±5m
A2	-0.975	0.001	±5m	-0.889	<0.001	±5m
A3	-0.999	0.001	±2m	-0.973	0.001	±3m
L1	-0.983	<0.001	±4.5m	-0.986	<0.001	±2.5m
L2	-0.972	0.006	±6m	-0.959	<0.001	±4m
L3	-0.997	<0.001	±2m	-0.963	<0.001	±2.5m
U1	-0.968	0.032	±8m	-0.981	<0.001	±2.5m
U2	-0.997	<0.001	±2m	-0.894	<0.001	±5m
U3	-0.984	0.016	±5m	-0.945	<0.001	±4m
U4	-0.997	<0.001	±2m	-0.997	<0.001	±1.5m
D	-0.979	0.004	±5m	-0.964	<0.001	±2.5m
Mean	-0.984		±4.2m	-0.951		±3.4m

Table 3. Mean (±SE) home range sizes of male and female bushy-tailed woodrats during 1992 - 94. Sample sizes are in parentheses; minimum and maximum home range sizes are shown in parentheses below mean values.

Year	Male Home range size (ha)	Female Home range size (ha)
1992	5.49 ± 1.48 (5) (1.59 - 9.18)	3.13 ± 0.65 (9) (1.65 - 6.90)
1993	5.10 ± 0.84 (8) (1.93 - 10.06)	3.15 ± 0.82 (9) (0.13 - 7.43)
1994	7.26 ± 0.70 (10) (3.84 - 11.19)	4.44 ± 1.33 (8) (0.91 - 10.44)

Table 4. Mean number of home ranges overlapped with (±SE) during the study period for each year and overlap category. Sample sizes are shown in parentheses.

Overlap Category	Year 1992	1993	1994
Male-male	2.0 ± 0.5 (5)	5.3 ± 0.5 (8)	8.0 ± 0.3 (10)
Male-female	4.2 ± 1.4 (5)	5.5 ± 0.7 (8)	6.3 ± 0.3 (10)
Female-female	6.0 ± 0.7 (9)	3.6 ± 0.6 (9)	5.0 ± 0.6 (8)
Female-male	2.3 ± 0.4 (9)	4.9 ± 0.4 (9)	7.9 ± 0.7 (8)

Table 5. Mean Cumulative Overlap Index (ΣOI) values ($\pm$SE) for each year. Letters indicate significant differences (Tukey-Kramer test) between pairs of values within a year that share the same letter. Sample sizes are shown in parentheses.

Overlap Category	Year 1992	1993	1994
Male-male	0.20 $\pm$ 0.04 (5)	0.63 $\pm$ 0.08 (8)	0.82 $\pm$ 0.10 (10) a
Male-female	0.40 $\pm$ 0.11 (5)	0.67 $\pm$ 0.08 (8)	0.70 $\pm$ 0.04 (10) b
Female-female	0.41 $\pm$ 0.07 (9)	0.53 $\pm$ 0.12 (9)	0.33 $\pm$ 0.05 (8) abc
Female-male	0.26 $\pm$ 0.08 (9)	0.60 $\pm$ 0.10 (9)	0.71 $\pm$ 0.13 (8) c

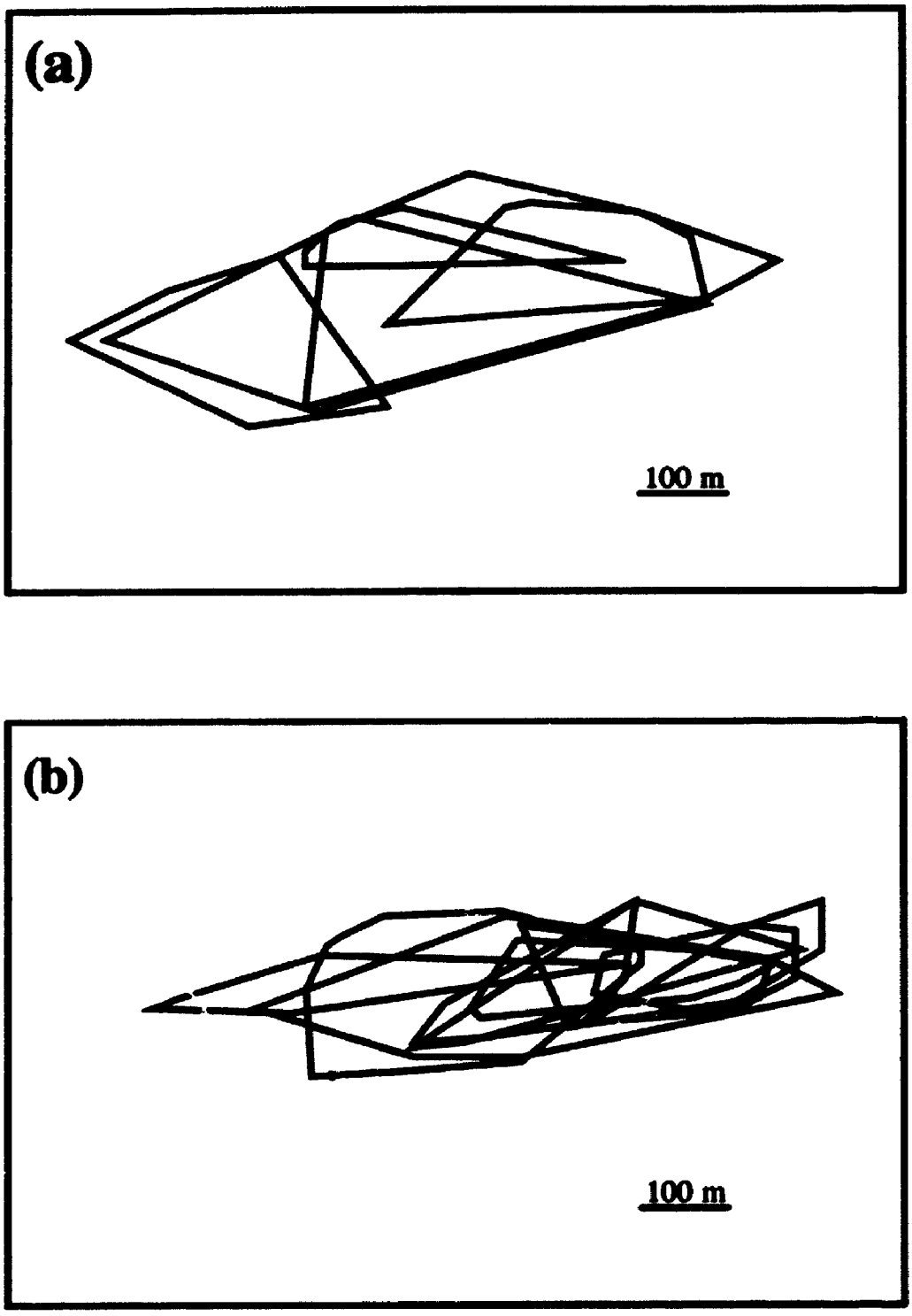

Figure 2. Minimum Convex Polygon home ranges for (a) males (n = 5) and (b) females (n = 9) in 1992.

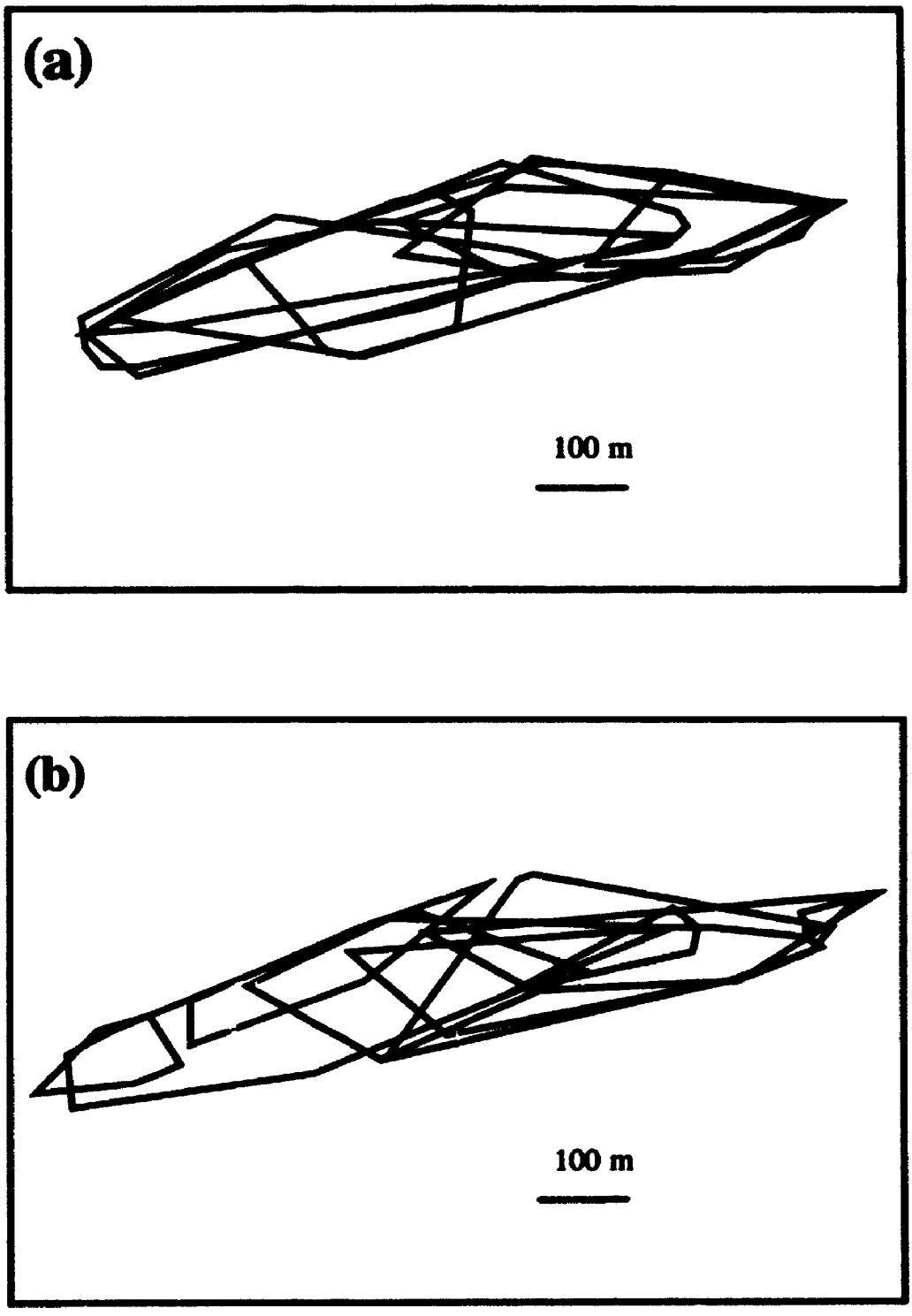

Figure 3. Minimum Convex Polygon home ranges for (a) males (n = 8) and (b) females (n = 9) in 1993.

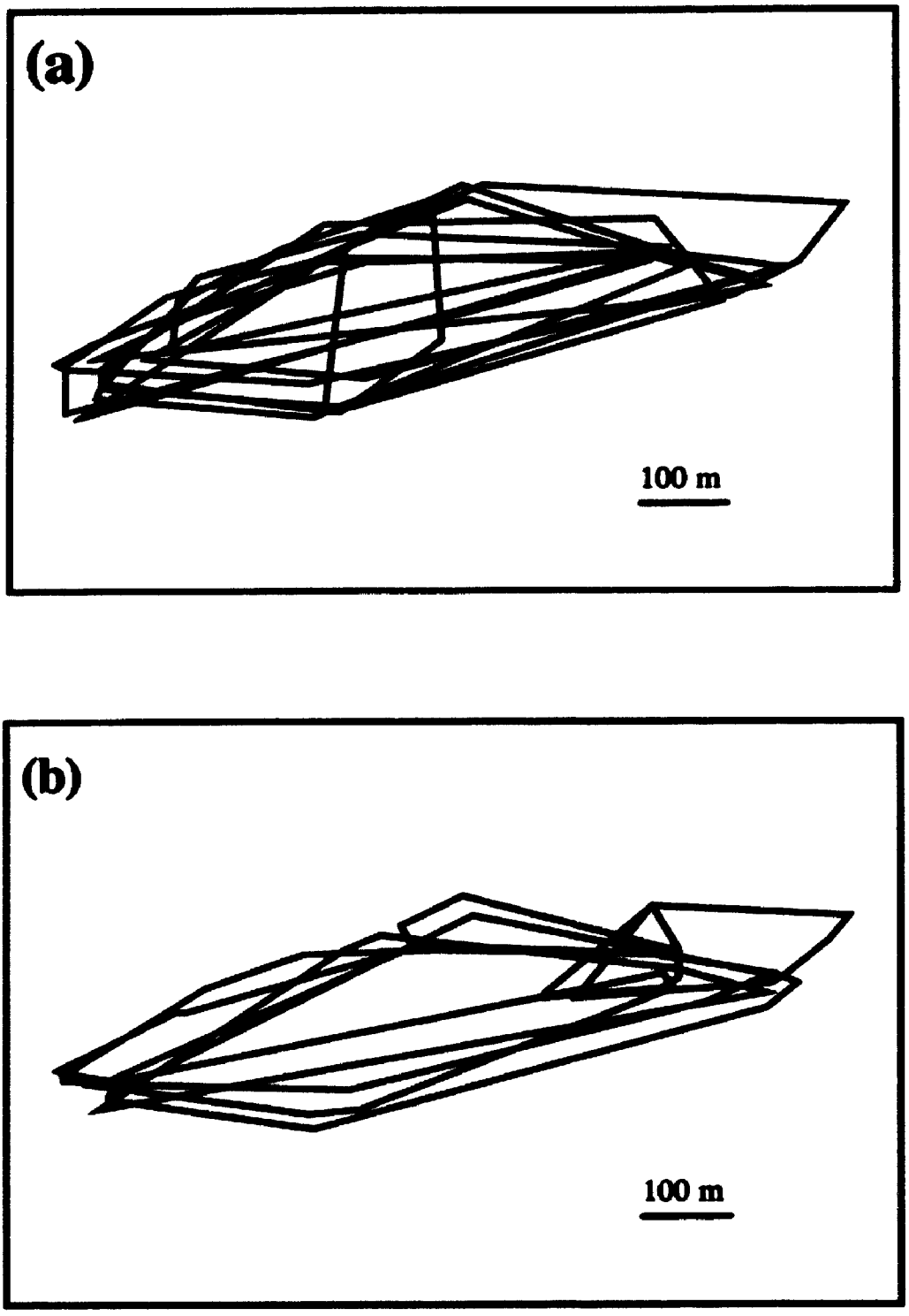

Figure 4. Minimum Convex Polygon home ranges for (a) males (n = 10) and (b) females (n =8) in 1994.

CHAPTER 4.

PATERNITY OF LITTERS AND THE MATING SYSTEM.

4.1 INTRODUCTION

Mammalian mating systems are classified by two measures; the distribution of reproductive success between the sexes, and the mating strategies employed by each sex to obtain matings. In general, the mating systems exhibited by mammals can be defined as follows. In a monogamous system, a single male and female have an exclusive mating relationship, and both males and females exhibit parental care (Wittenberger 1979). In the few (~5%) species of mammals that exhibit monogamy, biparental care is required for the successful rearing of offspring (Bekoff et al. 1984; Ribble 1991). In such situations, males often exhibit substantial parental care, which reaches the extreme situation of male lactation in the Dayak fruit bat (Francis et al. 1994). Because each litter results from an exclusive pair bond, the distribution and subsequent variation in reproductive success is even between the sexes. Any variation in reproductive success within the population can be attributed mainly to the differential survival of litters. The exclusive mating relationship, coupled with the lack of opportunity to obtain extra pair matings, results in both male and female mating strategies involving the choice of a suitable mate, because once the litter is born, both individuals must be committed to the shared parental duties, to ensure the survival of the litter. The characteristics of suitable mates that are favoured by the opposite sex may

vary between species and sexes, but body size (Shapiro and Dewsbury 1986; Solomon 1993), or mate quality (Ribble 1992) appear to be two of the more common characteristics that determine mate choice. In addition, the monogamous pair defend a common area to maximize the likelihood of offspring survival. Spatial defense ensures not only that sufficient food is reliably available for the growing litter, but also reduces the risk of infanticide from conspecifics (Wolff 1993).

Polygyny is defined by a prolonged and exclusive mating relationship between one male and two or more females. In such a system, all females that are capable of breeding will attempt to produce offspring. As a result, most of the variance in female reproductive success can be explained by factors affecting litter size (i.e., differential survival of offspring and fecundity of individual females). Variation in male reproductive success is usually much greater in a polygynous mating system than in a monogamous system, due to the fact that only the dominant males have the opportunity to mate. Males may directly defend the females as a resource, or may defend access to a resource required by females, such as food supply or nest sites. Because males restrict access to more than one female (up to 61 in a single harem for elephant seals; Le Boeuf and Reiter 1988), many males are unable to obtain mates, and will therefore gain no reproductive success. As a result, the distribution of male reproductive success is likely to be extremely skewed, and variance in male reproductive success will be high relative to female reproductive success. Despite the fact that only dominant males that are capable of resource defense appear to have the opportunity to obtain matings, the presence of more than one male mating strategy in the population may play a key role in reducing the variance in male mating opportunities. Subordinate males

that are unable to defend resources may still obtain matings by "sneaking" copulations when the dominant male is occupied with the defense of his resources against rivals. Such sneaking behaviour is usually exhibited by younger or smaller individuals (Le Boeuf 1974; Clutton-Brock et al. 1979), and may result in some fitness payoffs to those individuals that follow such a strategy. Alternative male strategies in polygynous systems are usually age-specific, in that dominant animals are usually old, and sneaky or satellite males are young. Therefore, in a polygynous system, the potential to exhibit alternate strategies other than defense of females or resources required by females, may have significant effects in shaping the reproductive behaviour of individual males.

In a promiscuous mating system, there is no prolonged association between the sexes, and members of at least one sex mate with multiple members of the opposite sex (Wittenberger 1979). Here, the distribution of reproductive success between males and females is hard to predict (Shields 1987). Female reproductive success is constrained physiologically, and all females that are capable of breeding usually do so. Because defense of females may or may not exist, mating opportunities within the broad category of promiscuous mating systems are extremely diverse. If mating opportunities are dominated by a few males that are able to monopolize mates, (at least during the estrus period of females), then the potential exists for male reproductive success to be extremely skewed, perhaps even more so than in a polygynous system. Given appropriate conditions (such as asynchronous and non-simultaneous estrus), it is technically possible for one male to father the litters of all females. However, if multiple males mate with a female, a single male is unlikely to gain exclusive paternity of her litter, and therefore, the distribution of male reproductive success may

be more uniform, and comparable to that of females. In keeping with the variation in allocation of reproductive success, both sexes may also show a variety of mating strategies within the broad definition of promiscuity. The strategy adopted by a female depends very much on whether one, or multiple males mate with her during estrus. If only one male mates with a female during estrus, the best situation for the female would be to mate with the highest quality male available. If females mate with multiple males, then females can be less choosy, since at least one of her mates would be expected to produce viable, high quality sperm. Male strategies within promiscuous systems range from courting and guarding a female during her entire period of receptivity (if females mate with only one male), to simply mating with as many females as possible (if females mate with more than one male), where paternity of juveniles is decided by sperm competition (Parker 1984; Parker et al. 1990).

In his review of mammalian mating systems, Clutton-Brock (1989) suggested that the majority of mating systems could be defined by three variables; the degree of paternal care, the stability of female groups and the spatial distribution of females. Despite investigations documenting these three variables, detailed descriptions of individual mating behaviour are scarce. Mating system theory is rapidly moving away from the idea that the mating system can and should be measured at the population level, as a result of the realization that the mating system of the population is the result of the behaviour of individuals that comprise a population. Therefore, the mating strategies and behaviour of individuals, rather than the pattern within the population should be the currency with which we investigate and define mating systems. Recently, such an approach to the study of mating systems has been facilitated by the increasingly widespread

use of genetic tools to determine parentage of offspring (see Avise 1994 for review). Techniques such as allozyme electrophoresis (Ostfeld et al. 1988; Xia and Millar 1989; Boellstorff et al. 1994) and multilocus DNA fingerprinting (Ribble 1991; Tegelstrom et al. 1991; Marinelli et al. 1992; McRae and Kovacs 1994; Stockley et al. 1994; Ribble and Millar, in press) have allowed accurate assessment of parentage and unambiguous determination of mating systems.

The study of mating systems provides information at two levels. First, because the mating system involves interactions between individuals within a population, it is affected by a variety of factors, such as habitat selection (Verner and Willson 1966), foraging behaviour (Emlen and Oring 1977), sex ratio (Fisher 1930), territoriality (Ostfeld 1985) and parental behaviour (Ribble 1991). As such, the study of mating systems involves a suite of widely-investigated and well-established theories (Trivers 1972; Charnov 1976; Frank 1990). Identification of the mating system also provides valuable information regarding the ecology and life-history of the species under investigation, particularly when data on parentage and kinship are included (Queller et al. 1993).

At a more theoretical level, detailed studies of mating systems allow the development of an integrated theory of mating system evolution (Emlen and Oring 1977; Wittenberger 1979). Attempts to construct such a theory by assimilating data from a variety of species/taxa have been relatively unsuccessful because many studies describe the mating system only in terms of the social organization within the population (Cameron and Spencer 1985; Ostfeld 1986; Randall 1991; Lambin et al. 1992). Such studies, while providing valuable information at the level of the study organism(s), are limited in their contribution to the development of a

unified theory, because they do not consider adaptation in terms of the individual genome (Hamilton 1964; Emlen and Oring 1977). Comparisons between studies on mating systems are only of value at the theoretical level when both the genetic fitness and the behaviour employed to maximize fitness by individuals are considered.

In Chapter 3, I found that, based on the spatial distribution and home range overlap within the population, the most likely mating system was promiscuity. However, spatial data alone cannot provide confirmation of the mating system, or determine the type of promiscuity that *N. cinerea* exhibits. The purpose of this chapter is to describe the genetic mating system of *N. cinerea* using DNA fingerprinting to determine the paternity of all juveniles born over the study period. By evaluating the variance in male reproductive success relative to that of females, and examining litters for evidence of multiple paternity, the pattern of male mating success and corresponding male mating strategies can be identified. This information then can be combined with the data from the previous chapter, to unambiguously determine the mating system of *N. cinerea*.

4.2 METHODS

4.2.1 Extraction, Restriction and Southern Transfer of DNA samples.

Tissue from ear clips (20 - 55 μg) was digested with 14μl of Proteinase K, added to 700 μl lysis Buffer (50 mM Tris-HCl, 50 mM EDTA, 100 mM NaCl, 1% SDS, 1% 2-mercaptoethanol) at 55°C (Ribble 1991). Incubation was carried out overnight, and one hour before the end of the digestion, 7μl of 10 μg/μl RNAse A was added. Genomic DNA was extracted by a series of reactions using phenol, phenol:chloroform, and chloroform. DNA was then precipitated in 100% ethanol, pelleted out via centrifugation, and suspended in 50μl of 1X TBE. Samples were stored at 4°C. 10 μg of genomic DNA was subsequently digested by adding *Alu I* to a solution containing 10 mM spermidine (Maniatis et al. 1982). Differential sized fragments within each digested sample were separated by electrophoresis (Thorne 1967), on a 15 cm x 20 cm 0.8% agarose gel for 18 - 20 hours @ 2 V/cm. Gels were then washed twice in denaturing solution (1.5 M NaCl, 0.5 M NaOH) resulting in single stranded DNA. This was followed by three washes in neutralizing solution (2.5 M ammonium acetate), after which the DNA was transferred to a nitrocellulose membrane (Schleicher and Schuell) by Southern transfer (Southern 1975), using 1 M ammonium acetate, 0.02 M NaOH.

4.2.2 RNA Hybridization of DNA.

I used an RNA template ([AGGGCUGGAGG]$_{54}$) analogous to probe 33.6 (Jeffreys et al. 1985a) in the hybridization reactions. This

minisatellite sequence is identical to the probe used by Ribble (1991), which has been shown to cross-hybridize with nucleotide sequences of many vertebrates (Burke and Bruford 1987; Westneat 1990; Ribble 1991; Wickings et al. 1993; McRae and Kovacs 1994; Millar et al. 1994). Although precautions must be taken when working with RNA, to prevent degradation, the resulting RNA-DNA hybrids formed during the hybridization reaction show greater thermal stability than DNA-DNA hybrids. This enables the blots to be washed at higher temperatures than DNA-DNA hybrid blots, resulting in less background radiation on the blots. The probe was radiolabelled with ^{32}P during a transcription reaction (Ribble 1991). Phenol:chloroform and chloroform extractions were used to remove any non-specific transcription. Membranes were exposed to a hybridization solution (5X SSPE, DI formamide, 1X Denhardts solution, 10μg/μl tRNA and dextran sulphate) containing the radiolabelled probe for 18 - 24 hours at 45°C. Membranes were then washed in 2X SSPE, 0.2% SDS at 55 - 65°C until background counts reached 1 - 3000 cpm, after which they were exposed to X ray film (Kodak X-OMAT AR) with intensifying screens for 5 - 25 days at -70°C.

4.2.3 Scoring of DNA Fingerprints.

Since female home ranges overlapped with the home ranges of more than one male (Chapter 3), assessment of a putative father based on behavioural data was not possible. Therefore, DNA samples from all resident males for a given year were run on gels containing the mother and offspring. Due to the large number of resident males in 1992 and 1994, multiple gels were run for each maternal lineage, to compare the

fingerprints from mother and juveniles with all potential fathers. Because of the high trapability of woodrats (Hickling 1987), I assumed that all potential fathers of a litter had been trapped at least once (i.e., there were no males present on the study area that were undetected). All radiographs were scanned on a Bio-Rad Gel Doc 1000 system, which allowed each lane of the gel to be scanned individually. The resultant output was an optical density graph, where the individual fingerprint consisted of a series of peaks, representing the bands. The Bio-Rad Gel Doc software permitted two or more graphs to be overlaid, resulting in accurate comparison of banding patterns. As restriction enzyme digests using *Alu I* resulted in a large number of small (< 2 kb) restriction fragments, bands were scored between 23 and 2 kb on all radiographs. Bands in the juveniles' lanes were assessed as either maternally or paternally derived, based on position ($\pm$ 1.0 mm; Burke and Bruford 1987) and intensity (height of the peak on the resulting graph).

4.2.4. Paternity Identification.

For the purpose of paternity identification, I considered only those bands that could not have derived from the mother, i.e., all bands that were either maternally inherited, or shared by the father and the mother. By considering only those bands in the fingerprint of the juvenile that could only have been transmitted from the father (diagnostic paternal bands), I identified a putative father. Males were considered as putative fathers if they possessed all diagnostic bands, or all but one diagnostic band, with the next closest male possessing 60% or fewer of the diagnostic bands. In this way, putative fathers could be identified, while allowing for the fact that

some bands in the fingerprints of juveniles may have resulted from mutation.

In order to determine whether the putative father could be reliably identified as the genetic father, I calculated the probability that (i) an unrelated male possessed all the diagnostic bands, and (ii) a related male possessed all the diagnostic bands. This value was calculated as $p = X^m$ (Jeffreys et al. 1985b), where X is the degree of band sharing among unrelated males, and m is the number of diagnostic bands employed in the identification of a putative father for each litter. In contrast, $p = ((1+X)/2)^m$ for related males (Hill 1986). Following Ribble (1991), I assumed equal allele frequencies, unlinked loci, and an equal probability of detecting differences across fragment sizes (Jeffreys et al. 1985a,b; Hill 1986; Cohen 1990).

4.3 RESULTS

4.3.1 Litter size and maternity.

A total of 58 juveniles from 35 litters were recorded. The number of litters, litter sizes, and mean litter size for all years are shown in Table 6. Birth dates for all juveniles were calculated using the formula from Moses (1992); if a litter consisted of more than one juvenile, the mean birth date was considered to be the parturition date. In 27 litters, the maternity of juveniles could be assigned, based on the capture location relative to the nest of a female, and the stage of reproduction of the female. In the remaining 8 litters, maternity was assigned to 1 of 2 potential mothers, whose nest sites and stage of reproduction were relatively close. In these cases, maternity was then assessed using DNA fingerprinting. The mean ($\pm$SD) genetic similarity (D) for all known mother-offspring pedigrees was 0.57 $\pm$ 0.08 (range = 0.40 - 0.71). This range of values was used to determine maternity in the 8 litters where maternity was uncertain. In these 8 litters, one female showed a genetic similarity value that was within the range of known values for first-order relatives; mean = 0.53 (range = 0.45 - 0.59), while the other female had a D value that was outside this range; mean = 0.29 (range = 0.17 - 0.38). The female with the largest D value was identified as the mother of the offspring, provided that the other female had a D value that fell outside the range of 0.40 - 0.71.

4.3.2 DNA Fingerprinting and paternity identification.

Pedigrees were analyzed by DNA fingerprinting for all 35 litters. The mean (±SE) number of bands scored for mothers, fathers and offspring are shown in Table 7. Having identified a putative father, the probability of having incorrectly identified him as the sire of the litter was calculated. The mean proportion of shared bands among 7 randomly chosen, and therefore, presumably unrelated males was found to be 0.14 (range: 0.05 - 0.25). Therefore, the chance of an unrelated male possessing the same diagnostic paternal bands ranged from 1.1×10^{-6} (7 paternal bands) to 2.2×10^{-14} (16 paternal bands). The corresponding calculation for related males showed that the probability of a related male having the same pattern of diagnostic bands ranged from 1.9×10^{-2} (diagnostic bands = 7) to 1.2×10^{-4} (diagnostic bands = 16). Given these probabilities and the fact that all resident males were included in the paternity analysis, I was confident that the putative father was the genetic father. Assuming correct maternity and paternity for all pedigrees, the mutation rate was 8.7×10^{-3} (14/1611). No more than one mutation was observed for any juvenile.

4.3.3 Characteristics of the mating system.

The pedigrees for all 35 litters are shown in the form of parental tables for 1992 (Table 8), 1993 (Table 9) and 1994 (Table 10). The distribution of reproductive success of males and females on the study area in all years is shown in Figure 5. Two way ANOVA revealed no significant differences in reproductive success between the sexes (F =

0.01; df = 1, 68; p = 0.97) or within years (F = 0.15; df = 2, 68; p = 0.86). The interaction between sex and year was not statistically significant (F = 0.84; df = 2, 66; p = 0.44). There was no bias in the age of individuals that failed to produce any offspring. Males: 7 adults and 8 yearlings, p = 0.5; Females: 5 adults and 2 yearlings, p = 0.227 (Binomial test).

Of the 35 litters born over the period of study, 17 consisted of 2 or 3 juveniles (Table 6). Within these 17 litters, there was no evidence for multiple paternity; one male sired all offspring in each litter. However, 6 females produced a second litter within a season, all of which were sired by a male that did not sire the first litter. In 5 of the 6 cases, the sire of the first litter was still present and reproductively active on the study area. In addition, 7 females produced litters in more than one year. In 4 of the litters, the sire of the litter from the previous year was no longer present on the study area. However, in the other 3 cases, the previous mate was present, yet the litter was fathered by another male.

Male-female pairings based on DNA figerprinting, the outcrops on which they were resident, and the estrus periods of females prior to conception are shown in Tables 11 - 13. As can be seen from Tables 11 - 13, 23 of 35 (65.7%) litters were produced by a male and a female from the same outcrop. The remaining 12 litters resulted from matings between animals from adjacent outcrops. If an outcrop had more than one resident female, no male was able to monopolize all the females on the outcrop, even if he was the only resident. Despite the overall asynchrony in estrus shown by females in the population, two or more females may be in estrus simultaneously (Tables 11 - 13).

4.4 DISCUSSION

Lack of multiple paternity within litters is consistent with two possible mating strategies. One involves females that mate only with one male during each period of estrus, with some form of exclusive access being gained by the male. The alternative involves females mating with more than one male, with paternity being decided by sperm competition (Parker 1970; Birkhead and Møller 1993; Gomendino and Roldan 1993). On the basis of the available data on *N. cinerea*, there is evidence that males guard females during estrus. Lab studies have demonstrated that copulation in *N. cinerea* is extremely rapid, and may be repeated up to 5 times in a 10 minute period (Escherich 1981). Escherich (1981) also suggested that due to the degree of chasing involved during courtship, copulation probably takes place away from the nest. Female bushy-tailed woodrats undergo a postpartum estrus of 4 - 6 days (Egoscue 1962; Escherich 1981), and lab studies have indicated that many females became pregnant soon after (24 - 48 hours) birth of the previous litter (Escherich 1981). Therefore, in order for a male to monopolize access to an estrus female, he would only have to prevent other males from mating with her for a short time period. Using data from this study where females produced two litters in a season, and assuming a gestation period of 30 days (Escherich 1981), the mean interval between parturition of the first litter and conception of the second was found to be 6.5 days (range: 1 - 13 days). Assuming that females are in estrus for all or part of this period means that the time males spend associating with a single female is relatively short in relation to the duration of the breeding season. Data on the nocturnal activity and locations of woodrats from radiotelemetry also

supports the hypothesis that males guard females during estrus. Due to the fact that radiotelemetry was carried out on each outcrop only once per week, positional data on females and males during the majority of the estrus periods were missed. However, radiotelemetry provided information on the locations of three male-female pairs during estrus periods that preceded a successful litter. In 1993, male-female pairs were found to be an average of 15m apart over a 8 minute time period. In 1994, locations of 2 male-female pairs were recorded during estrus; they were separated by an average of 16m (over 10 minutes) for both pairs of individuals. Although these findings represent only 9% of all litters, they show that during the period of estrus, male-female pairs that subsequently produce offspring were found in extremely close proximity. Mate exclusiveness may also be ensured by the formation of copulatory plugs, which were occasionally observed during livetrapping.

Given that male bushy-tailed woodrats have the potential to gain exclusive access to a female during estrus, males may be unable to maintain access to more than one female at a time. The estrus periods of different females that mated with the same male (Tables 11 - 13) showed a similar pattern in that they were separated by a mean duration of 18.5 days (range 5 - 40 days), which is at least the duration of one estrus period. Furthermore, when two females on the same outcrop underwent estrus at similar times, each had their litter sired by a different male (Tables 11 - 13). This suggests that once a male has committed himself to courting and/or guarding a female to achieve exclusive access and ensure paternity, he must remain with her during her period of nocturnal activity for the entire estrus, or at least until a copulatory plug has formed, preventing other males from mating that night. By making such a commitment, the

male will be unable to mate with other females that enter estrus at the same time. The male must therefore wait until his present mate is no longer receptive before he can move on in search of other females.

The accuracy of such assumptions can be tested by investigating the probability of observing single paternity, even if more than one male mates with a female during a single estrus period. Mammalian ova are ovulated and fertilized simultaneously, therefore, multiple paternity will only result if viable sperm from more than one male are present in the oviduct at the time of ovulation (Gomendino and Roldan 1993). It has been suggested that sperm competition in mammals resembles a raffle, where the male with the largest amount of sperm is more likely to fertilize the ova (Parker 1984; Parker et al. 1990). As a conservative estimate, I consider a scenario where, if multiple mating occurs, two males mate with a female. The probability of male k siring all juveniles within a litter is p_k^n, where n is the litter size. Therefore, within a litter, the probability of observing single paternity is $\Sigma(p_k^n)$. No information is available on ejaculate volumes in *Neotoma*, so probabilities of paternity were obtained from Pierce et al. (1990), where ejaculate volume of four vole species was measured, and where the average differential allocation of sperm within the species was 0.59 : 0.41. Therefore, I set $p_1 = 0.59$, and $p_2 = 0.41$, as the probabilities that males 1 and 2 fathered a juvenile. The probability of observing single paternity is therefore 0.52, and 0.28, for a litter size of 2 and 3, respectively. From these values, the probability of observing multiple mating within a litter can be calculated as $P_{mult2} = (1\text{-}0.52) \times R$ for litters size of 2, and $P_{mult3} = (1\text{-}0.28) \times R$ for litter sizes of 3, where R is the proportion of litters that involve more than one male mating with a female. From this, the probability of not detecting at least one litter with

multiple paternity (P_{nm}), can be calculated as $(1-P_{mult2})^{L2} \times (1-P_{mult3})^{L3}$, where L2 and L3 are the number of litters of size 2 and 3, respectively. The probability of detecting multiple paternity is $(1 - P_{nm})$, or P_m. Figure 6 shows the probability of detecting multiple paternity (P_m) when females mate with more than one male in 0 - 100% of litters. In small mammals, the minimum proportion of litters where more than one male mates with the female has been calculated as 25% for *Peromyscus leucopus* (Xia and Millar 1991), 33% for *Microtus pennsylvanicus* (Boonstra et al. 1993), and 22% for *Peromyscus maniculatus* (Ribble and Millar, in press). Therefore, for the purpose of this study, I examined the probability of detecting multiple paternity where the proportion of litters resulting from multiple matings was 20 - 30% (Figure 6). Using this conservative estimate, the probability of detecting multiple paternity was 0.87 - 0.96. As no multiple paternity was observed, I suggest that there is strong evidence to assume that all litters investigated in this study were the result of a single male mating with a female, where paternity was ensured by mate guarding and/or copulatory plugs.

There was no significant difference in the variance in reproductive success of males and females either within or between years. At least 75% (Tables 8 - 10) of females produced a successful litter in each year of study, and all resident females were observed to undergo at least one estrus. Any variation in reproductive success of females appears to be due to the differential survival of litters, rather than the opportunity to breed (Moses 1992). Females that failed to produce any offspring that survived until weaning fell into two categories: those that did not become pregnant (either not undergoing estrus or undergoing estrus but failing to become pregnant), and those who produced litters that did not survive (i.e.,

recorded as pregnant, but no pups captured). Although the proportion of males achieving successful matings was lower (57 - 63%; Tables 8 - 10), the variation in reproductive success was similar between the sexes in all years, indicating that among males, the distribution of reproductive success and mating opportunities is relatively broad. Because males do not appear to be capable of courting more than one female at a time, the wide distribution of mating opportunity among males is not surprising.

The pattern of male mating success observed in this study, coupled with the fact that males and females show similar variance in reproductive success suggests that (i) males gain exclusive access to females during estrus, and (ii) males are unable to interact with more than one female at a time. Such a pattern of male reproductive behaviour suggests either serial (or facultative) monogamy (where females mate with a single male during each receptive period, but mate with different males over successive receptive periods), or roving male promiscuity (where males rove widely in search of individual females, which they defend for all or part of their receptive period) (Clutton-Brock 1989). To determine which mating system and therefore which male reproductive strategies operate in this population, the size of occupied space and the social behaviour of the females must be considered. For serial monogamy to arise, females usually have home ranges that are small enough to be overlapped by the home range of a male (Ostfeld 1985). Males are therefore able to defend the female over her entire range, and gain exclusive access during estrus. In contrast, the behaviour of females in a system where roving male promiscuity would be favoured is markedly different. If females range widely, and are distributed unpredictably, simultaneous defense of the occupied space of more than one female by a male at any given time is impossible (Emlen and Oring

1977). Under these conditions, the best mating strategy for males is to attempt to defend estrus females during all or part of their receptive period. Even though the nests of female bushy-tailed woodrats are spatially aggregated on outcrops, the relatively large home ranges of females (mean = 3.56 ha), and their extended foraging movements from the nest during the breeding season result in a situation where males are unable to simultaneously defend access to multiple females over their entire range. Males can only secure access to females by maintaining close proximity to a single female during their short estrus periods. In addition, despite the fact that males have larger home ranges than females, and overlap the home ranges of multiple females, an apparent lack of male territoriality results in several males overlapping with each female. As such, even when female home ranges are small, males are unable to maintain exclusive access simply by defending the home range of the female. Therefore, the pattern of mating success, coupled with the economic defensibility of females leads to the conclusion that bushy-tailed woodrats exhibit a roving male promiscuous system, where males defend access to individual females during estrus. Whether males gain exclusive access to females cannot be determined unequivocally by this study, but the available evidence is highly suggestive of such a scenario (Fig. 6). A similar form of mating system has been described for a diverse group of mammals, including moose (Peterson 1955), polar bears (Ramsay and Stirling 1986) and orang-utans (MacKinnon 1974), which all show similar characteristics of roving, non territorial males, and dispersed or spatially unpredictable and therefore non-defensible females. In common with many mammals, it is the behaviour of the females in terms of their spatial distribution and economic

defensibility (Clutton-Brock 1989) that ultimately appears to determine the mating system of bushy-tailed woodrats.

In comparing the findings of this study with the mating systems of other species that live in rock piles and cache food, there appear to be differences between *N. cinerea* and ecologically similar species. American pikas *(Ochotona princeps)* have been reported as exhibiting either facultative monogamy or polygyny within a population, with females showing strong choice for particular males (Brandt 1989). Marmots also appear to exhibit mixed strategies within a population, with both monogamy and polygyny reported for yellow-bellied (Armitage 1975), and hoary marmots (Holmes 1984). Similar species outside North America, such as the rock hyrax *(Procavia capensis)* also appear to exhibit both monogamy and polygyny within colonies (Olds and Shoshani 1982). However, it must be stressed that mating systems in these species have been inferred from the spatial distribution and social interactions within the population. Given that the ecology of these species is so similar to *N. cinerea*, information on the reproductive success of individuals might alter the classification of the mating system for these species.

Table 6. Number of litters where at least one individual survived until weaning, litter size frequency and mean litter size of female bushy-tailed woodrats over the period of study (1992 - 94).

		Litter size			Mean
Year	N	1	2	3	litter size
1992	14	7	5	2	1.6
1993	11	7	2	2	1.6
1994	10	4	4	2	1.8
Total	35	18	11	6	1.7

Table 7. Summary of gel scoring data. The mean (±SE) number of bands scored for mother, fathers and juveniles across all gels. The mean (±SE) number and proportion of bands shared with parents and juveniles for both mothers and fathers are also shown. Ranges are in parentheses.

	Mother (N = 35)	Father (N = 35)	Juvenile (N = 58)
Mean (±SE) number of scoreable bands	28.3 ± 0.7 (16 - 37)	28.3 ± 1.2 (18 - 38)	27.8 ± 0.8 (17 - 39)
Mean (±SE) number of juvenile bands shared.	16.3 ± 0.6 (8 - 27)	11.3 ± 0.3 (7 - 16)	
Mean (±SE) proportion of juvenile bands.	0.58 ± 0.01 (0.47 - 0.73)	0.41 ± 0.01 (0.27 - 0.53)	

Table 8. Parental Table for 1992. The number of offspring produced by each male-female pair is shown, along with the reproductive success for each male (Ml RS) and female (Fm RS) for the 1992 breeding season. Numbers across the top and sides of this table are identification numbers for individual animals.

		MALES													Fm
		01	09	15	18	20	21	27	28	36	46	86	87	91	99	RS
FEMALES	11						2									2
	25				2											2
	30										1					1
	38															0
	39								1					1		2
	42										2					2
	44															0
	45					1										1
	49															0
	52															0
	58						2					3				5
	61				2											2
	62								1							1
	75											3				3
	93						1									1
	96												1			1
Ml RS		0	0	0	4	1	5	0	2	0	3	6	1	1	0	

Table 9. Parental Table for 1993. The number of offspring produced by each male-female pair is shown, along with the reproductive success for each male (Ml RS) and female (Fm RS) for the 1993 breeding season. Numbers across the top and sides of this table are identification numbers for individual animals.

		MALES								Fm
		27	28	87	99	117	133	154	194	RS
FEMALES	30		1							1
	42									0
	45					2	1			3
	58			3			3			6
	61		2							2
	62			1						1
	69					1				1
	78	1								1
	96									0
	106			1						1
	161					1				1
Ml RS		1	3	5	0	4	4	0	0	

Table 10. Parental Table for 1994. The number of offspring produced by each male-female pair is shown, along with the reproductive success for each male (Ml RS) and female (Fm RS) for the 1994 breeding season. Numbers across the top and sides of this table are identification numbers for individual animals.

		MALES													
		27	87	99	117	164	419	428	431	434	448	576	592	594	596	Fm RS
FEMALES	45			1												1
	62	1														1
	401							2								2
	416							2	2							4
	442															0
	582									2						2
	595														3	3
	718										1					1
	795									1				3		4
Ml RS		1	0	1	0	0	0	4	2	3	1	0	0	3	3	

Table 11. Estrus periods and female-male pairings that successfully produced offspring in 1992. The outcrop on which each animal was resident is given in brackets after the identification number (See Fig. 1). First and second litters within a year are indicated by I and II, respectively.

Female	Estrus (Julian days)	Male
6075 (LC)	99 - 103	6086 (LC)
6058 I (LC)	100 - 104	6021 (LC)
6045 (Deer)	105 - 109	6020 (Deer)
6030 (Arm)	117 - 121	6046 (Arm)
6039 I (Arm)	117 - 121	6091 (Arm)
6062 (Arm)	125 - 129	6028 (Arm)
6011 (Deer)	127 - 131	6021 (LC)
6025 (UC)	129 - 133	6018 (UC)
6093 (UC)	138 - 142	6021 (LC)
6061 (Arm)	140 - 144	6018 (UC)
6058 II (LC)	143 - 147	6086 (LC)
6096 (Arm)	144 - 148	6087 (Arm)
6042 (Arm)	147 - 151	6046 (Arm)
6039 II (Arm)	160 - 164	6028 (Arm)

Table 12. Estrus periods and female-male pairings that successfully produced offspring in 1993. The outcrop on which each animal was resident is given in brackets after the identification number (See Fig. 1). First and second litters within a year are indicated by I and II, respectively.

Female	Estrus (Julian days)	Male
6045 I (Deer)	122 - 126	6133 (LC)
6058 I (LC)	122 - 126	6087 (UC)
6030 (Arm)	127 - 131	6028 (Arm)
6069 (Deer)	134 - 138	6117 (Deer)
6061 (Arm)	140 - 144	6028 (Arm)
6062 (Arm)	141 - 145	6087 (UC)
6106 (UC)	151 - 155	6087 (UC)
6161 (LC)	153 - 157	6117 (Deer)
6058 II (LC)	155 - 159	6133 (LC)
6078 (UC)	168 - 172	6027 (LC)
6045 II (Deer)	186 - 191	6117 (Deer)

Table 13. Estrus periods and female-male pairings that successfully produced offspring in 1994. The outcrop on which each animal was resident is given in brackets after the identification number (See Fig. 1). First and second litters within a year are indicated by I and II, respectively.

Female	Estrus (Julian days)	Male
6795 I (LC)	102 - 106	6434 (LC)
6062 (Arm)	109 - 113	6027 (Arm)
6582 (UC)	111 - 115	6434 (LC)
6416 I (LC)	115 - 119	6431 (LC)
6595 (UC)	117 - 121	6596 (UC)
6718 (Deer)	120 - 124	6448 (LC)
6401 (LC)	122 - 126	6428 (UC)
6045 (Deer)	138 - 142	6099 (Deer)
6416 II (LC)	143 - 147	6428 (UC)
6795 II (LC)	143 - 147	6594 (LC)

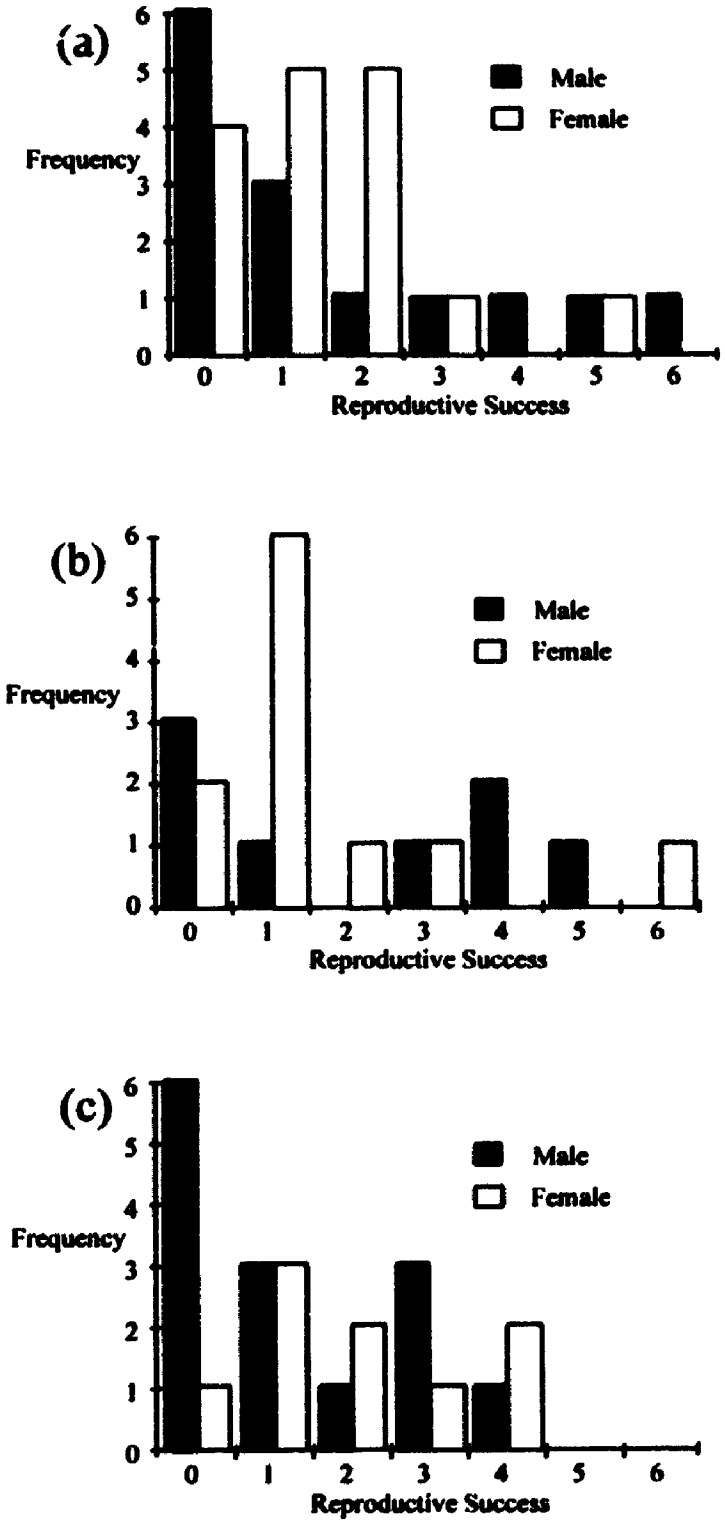

Figure 5. Distribution of male and female reproductive success (total number of offspring produced) in (a) 1992, (b) 1993 and (c) 1994.

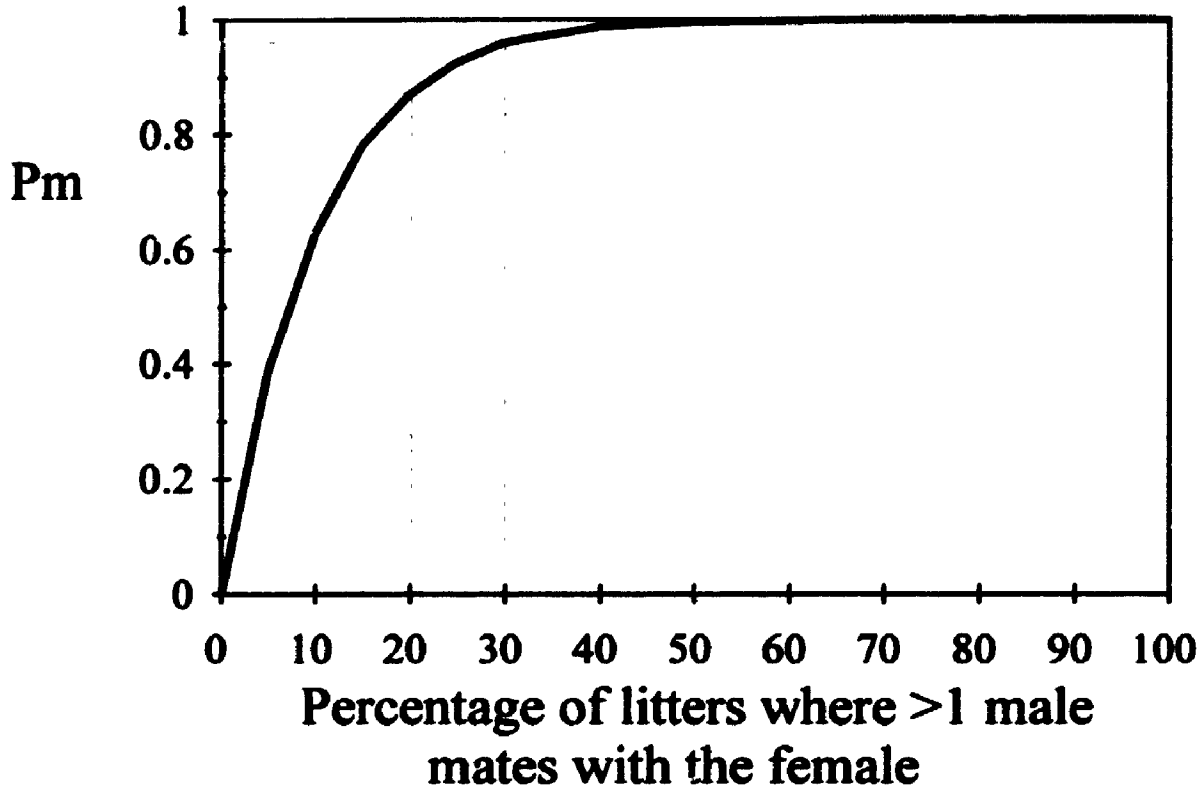

Figure 6. The probability of detecting multiple paternity (Pm), when females mate with two males in 0 - 100% of litters. The probability of detecting multiple paternity if 20 - 30% of litters result from more than one male mating with the female is shown by dashed lines (0.87 - 0.96). The number of litters with >1 offspring totaled 17 for this study (48.5% of litters).

CHAPTER 5.

MALE REPRODUCTIVE SUCCESS AND INTRASEXUAL COMPETITION.

5.1 INTRODUCTION

The energetics of mammalian reproduction, coupled with the differential patterns of parental investment between males and females have led to markedly different reproductive strategies between the sexes in the majority of mammalian species (Ridley 1978; Clutton-Brock 1989). Due to the high energetic costs and lengthy duration of gestation and lactation, the number of offspring that a female can produce is limited by her physiological and energetic capacity (Williams 1966). As such, females maximize reproductive success by investing heavily in their litters (Millar 1977; Merson and Kirkpatrick 1983; Bronson and Marsteller 1985; Trillmich 1986), and mating with the highest quality male available (Le Boeuf 1974; Clutton-Brock et al. 1982; Halliday 1983). In contrast, the males of over 95% of mammalian species exhibit no parental care (i.e., males in polygynous and promiscuous mating systems), and because their only form of investment in offspring is sperm (Ridley 1978; Clutton-Brock 1991), males have the potential to produce offspring with more than one female within a breeding season (Williams 1966). This differential parental investment was first addressed by Trivers (1972), who suggested that in species where one sex invests more (in this case, female mammals), members of the opposite sex will compete for access to them; for this

reason, they are termed the limiting sex (Williams 1966; Trivers 1972). As a consequence, the more successful males will be those that are able to acquire more than one mate during a breeding season. Males that possess a competitive advantage will gain access to more females, and thus have greater fitness. The establishment and maintenance of traits that confer such an advantage is usually the result of sexual selection (Darwin 1871; Andersson 1994).

The types of traits favoured by selection depends to a large extent on the mechanism of male-male competition within the population. Andersson (1994) identified five different mechanisms of male-male competition (scramble, endurance rivalry, contest, mate choice (indirect male competition) and sperm competition) along with the traits that would be favoured under each mechanism of competition. In a scramble competitive system, where reproductive success is maximized by traits that increase the ability of a male to locate females, close proximity to and/or frequent interactions with multiple females would be favoured (Schwagmeyer and Woontner 1986). Therefore, males would be under selective pressure to maintain close proximity to a number of females through choice of an appropriate nest site, or establishment of a large home range (Ostfeld 1986; Schwagmeyer 1988; Ryser 1992). If competition results from differences in the duration of sexual activity, then males that remain reproductively active for a long period of time would have greater reproductive success than those that were only capable of reproducing for a shorter time. Under this mechanism of male intrasexual competition, selection would favour the ability of males to successfully breed with females over an extended period of time (Campagna and Le Boeuf 1988; Appollonio et al. 1989). Direct contests between males, where the opportunity to breed with females is

restricted to dominant males, would favour traits (e.g., large body size or increasing weaponry) that improved success in direct confrontations (Clutton-Brock et al. 1982; Schwagmeyer and Brown 1983; Wickings et al. 1993). If males compete for females via female mate choice, the decision rests with the female, who will mate with the highest quality male available. As such, morphological or behavioural traits that reflect the quality of the male, or the ability of the male to provide some form of paternal investment (e.g., territory quality, nuptial gift) could result in a competitive advantage (Kitchen 1974; Huck et al. 1981; Shapiro and Dewsbury 1986). Finally, males may compete via sperm competition, where males either prevent rivals from mating by guarding, frequent copulation, or the production of copulatory plugs (Ridley 1983; Birkhead and Møller 1992), or displace or outcompete rival sperm (Parker 1970; Birkhead and Møller 1993). Under this mechanism of male-male competition, characteristics that improve the ability of the male to restrict mating opportunities for other males or ensure any mating order advantage would be favoured. Despite differences in the competition mechanisms, and the varied ways in which a trait could be favoured, the same trait may be selected under more than one mechanism of intrasexual competition among males, e.g., large body size may be favoured by both contest and mate choice competition scenarios (Clutton-Brock et al. 1982).

In Chapter 4, it was found that bushy-tailed woodrats exhibit a mating system that can best be described as roving male promiscuity, where females are widely and unpredictable dispersed, and males gain exclusive access to individual females during their estrus. As such, reproductive success is likely to be correlated with traits associated with female mate choice and sperm competition/mate guarding. In contrast,

traits associated with scramble and contest competition should show no relationship with reproductive success. The purpose of this chapter is to examine the relationship between male reproductive success and traits associated with different mechanisms of male competition. The degree to which reproductive success is correlated with traits hypothetically related to the various mechanisms of male intrasexual competition will determine (i) which male traits confer a competitive advantage, leading to increased reproductive success, and (ii) the manner by which male bushy-tailed woodrats compete for mates. I tested the hypotheses that, due to the mating system exhibited by *N. cinerea*, variation in the expression of traits associated with mate choice and sperm competition/mate guarding will show significant correlations with reproductive success, while traits associated with scramble, reproductive endurance and contest mechanisms of competition will show no relationship with reproductive success.

5.2 METHODS

5.2.1 Male Reproductive success.

Reproductive success was defined as the total number of offspring sired by each male that emerged from the natal nest following weaning in each year. Although it has been argued that reproductive success should be measured over the lifespan of individuals (Clutton-Brock 1988), data gathered on a number of individuals at a given time may be more effective at determining alternative male reproductive strategies, particularly those where the lifespan of the study species is short. A total of 29 reproductively active males were recorded over the course of this study, but only 5 were present in more than one year. Woodrats rarely move from the area in which they first establish as adults (Hickling 1987), so males that were not recorded in subsequent years were assumed to have died. Therefore, reproductive success within a year was used as the currency with which to investigate correlates of reproductive success.

5.2.2 Mechanisms of Male Intrasexual Competition.

For each mechanism of male-male competition in woodrats, measurable traits were identified (Table 14). Variables associated with scramble competition were defined as the number of female nests within 100m of a male nest, and the home range sizes of males. Nest sites of males and females were located by daytime radiotelemetry, and positions recorded on a scale map of the study area. The number of female nests within 100m of the male nest site (F100) could then be determined for each

resident male. The home range size of males was also examined as a trait that could potentially determine the number of females accessed by males. The reproductive endurance of males was defined as the time between first and last capture on the study area while having scrotal testes (i.e., in breeding condition). Body size and weight of males were obtained from routine measurements during livetrapping, and were defined as the mean head+body length and the mean weight while having scrotal testes. As woodrats do not breed in the year of their birth (Moses 1992), reproductive success was also examined in relation to age, where males were classed as either yearlings (1 year old) or adults (at least 2 years old). An index of male quality was defined as the growth rate of males during the breeding season. This index was calculated by fitting a regression line to a plot of male body weight while scrotal against Julian day. Because only males with >2 captures were used in this analysis, $N = 30$. The slope of the regression was then taken as an index of the growth rate, because it describes the rate at which males gained or lost weight during the breeding period. Growth rate was used as an indicator of male quality because males that were capable of gaining weight while maintaining a home range and searching for females were presumably in better condition than males that lost weight. Finally, the potential for males to sequester females was expressed as the degree to which male nests were spatially distributed. The number of male nest sites within 100m of the nest of a focal male (M100) was taken as a measure of the focal males' ability to monopolize access to neighbouring females. In addition, variance in mating success (defined as the number of females that a male successfully mated with) was examined as a predictor of variance in reproductive success.

Analyses of reproductive success in relation to the above traits were performed by correl tion and regression analysis or Student's t-tests (Zar 1984). Statistical significance was accepted at $p \leq 0.05$.

5.3 RESULTS

5.3.1 Male Reproductive success.

The reproductive success of all resident males in each year of study is shown in Figure 7. The mean (±SD) male reproductive success was 1.6 ± 2.1 (range: 0 - 6) in 1992, 2.0 ± 2.0 (range: 0 - 5) in 1993, and 1.3 ± 1.4 (range: 0 - 4) in 1994. There were no significant differences in the variance of reproductive success (Variance ratio test: Zar 1984) between either 1992 and 1993 ($F = 1.06$; $df = 14,8$; $p > 0.5$), 1993 and 1994 ($F = 1.94$; $df = 8,14$; $p > 0.2$), or 1992 and 1994 ($F = 2.06$; $df = 14,14$; $p > 0.1$). A significant correlation was found between the number of mates and reproductive success ($N = 36$, $r = 0.9$, $p < 0.001$) (Figure 8). As such, much of the variance in the reproductive success of males within a year (81%) can be explained by variation in mating success. Therefore, reproductive success appears to be an appropriate currency with which to measure the degree of male-male competition, as it is highly correlated with the number of mates that each male is able to acquire.

5.3.2 Mechanisms of Male Intrasexual competition.

The mean (±SD) and range of all variables analyzed in relation to reproductive success are shown in Table 14. Reproductive success was not significantly correlated with proximity to female nests ($p = 0.716$), or reproductive endurance ($p = 0.399$) (Table 14). Furthermore, reproductive success was not correlated with morphological and behavioural traits, such as weight ($p = 0.730$), body length ($p = 0.670$), or home range size ($p =$

0.523) (Table 14). However, reproductive success was significantly correlated with the growth rate ($p = 0.049$), and the number of male neighbours within 100m ($p = 0.013$) (Table 14). Figure 9 shows the positive relationship between growth rate and reproductive success, while the negative relationship between reproductive success and the number of male nests within 100m for each male is shown in Figure 10. Age had no effect on reproductive success ($t = 0.57$, $df = 32$, $p = 0.58$); adults (mean = 1.42, SE = 0.40, n = 19) and yearlings (mean = 1.76, SE = 0.46, n = 17) had similar reproductive success in all years.

5.4 DISCUSSION

Traits associated with mechanisms of scramble competition, reproductive endurance, and contest competition showed no statistically significant relationship with male reproductive success (Table 14). In contrast, reproductive success was positively correlated with male quality (i.e., growth rate; Table 14). The relationship between growth rates of males and reproductive success revealed two points of interest related to the reproductive ecology of male woodrats. First, successful males do not suffer any costs in terms of loss of condition (body weight) as a result of seeking, courting and copulating with females. Such an observation is in direct contrast to studies on other mammals, which demonstrate that due to the energetic costs of male-male rivalry, males may experience substantial weight loss (Clutton-Brock et al. 1982; Anderson and Fedak 1985; Deutsch et al. 1990). Second, growth rate in male woodrats is a more reliable predictor of reproductive success than body length or weight. The greater reproductive success of males with higher growth rates is likely a reflection of the quality of the male. Since females have no way of assessing growth rates, they may be choosing males based on some other indicator of quality such as vigor of display. Laboratory studies of *N. cinerea* demonstrate strong evidence of female mate choice, with documented cases of females either soliciting matings from males, or vigorously rejecting males despite being paired for up to 3 days (Escherich 1981). Therefore, given that lab studies are suggestive of female choice, and that male reproductive success correlates with a potential indicator of male quality, variance in male reproductive success appears to be at least partly the result of female mate choice, rather than male contests. The ways in which females are able to

assess male quality is unknown, but given the significant relationship between male growth rate and reproductive success, they appear to use a reliable indicator.

Reproductive success showed a negative relationship with the potential for competition or interference from neighbours (i.e., the number of males within 100m; Table 14). Male woodrats with fewer male neighbours within 100m had higher reproductive success than those with more neighbours. However, reproductive success showed no correlation with the number of females within 100m of male nest sites, indicating that in terms of nest site location, the number of competitors in close proximity is more important in determining reproductive success than the number of potential mates (Table 14). The density of nest sites also appears to have no effect on this relationship. A multiple regression of reproductive success on both M100 and F100 reveals that while a correlation still exists with M100 (t-ratio = 2.57; p = 0.015), there is no significant relationship with F100 (t-ratio = 0.17; p = 0.867). The relationship between reproductive success and the number of males within 100m supports the theory of male competition by mate guarding or attendance; males that have fewer competitors in close proximity obtain greater fitness, presumably because they are less likely to be disturbed by conspecifics while courting or mating with an estrus female. An interesting aspect of the relationship between proximity of competitors and reproductive success is that suitable nest sites for bushy-tailed woodrats consist of crevices in rocky outcrops or bluffs, and cannot be constructed by the woodrats (Finley 1958; Escherich 1981). The availability of suitable crevices places an upper limit on the number of nest sites on a particular outcrop. Males are not able to dictate the location of their nests, so they are unable to establish a nest in close proximity to

females unless a suitable nest site is available. Since nest sites are a limiting resource for *N. cinerea* (Hickling 1987), and obtaining shelter is vital due to an enhanced ability to conserve energy while in a nest (Brown 1968), individuals are presumably under pressure to locate a suitable nest as quickly as possible. Therefore, rather than gauging the location and population density of females before choosing a nest site, males may select a nest site based on the lack of competitors in close proximity.

In *N. cinerea*, reproductive success appears to be significantly correlated with traits associated with female mate choice and mate guarding competition mechanisms, while no relationship is shown between reproductive success and traits associated with scramble, endurance or contest competition. While significant relationships exist between reproductive success and certain traits exhibited by male woodrats, these traits may not necessarily be the result of sexual selection. While it is widely accepted that traits that correlate with reproductive success are often the result of sexual selection, many traits that increase the mating success of males may also be favoured through natural selection (Endler 1986). Therefore, a trait should only be classed as sexually selected if it confers an advantage in male-male competition, and would not be favoured under natural selection (Andersson 1994). As no information is available on the relative costs of possessing such traits, I am therefore hesitant to refer to them as sexually selected traits. However, regardless of how such traits evolved, the significant relationships between such male traits and reproductive success indicates that the expression of these traits confers a competitive advantage (in terms of greater reproductive success) to those males that possess them. As such, these traits would be expected to be selected for, and maintained in male bushy-tailed woodrats.

Table 14. Traits investigated in relation to reproductive success for each mechanism of male-male competition. Mean, standard deviation and range are given for each trait. The Pearson product-moment correlation coefficient (r) and the probability value obtained from regression of each trait on reproductive success are also shown. Statistically significant correlations are marked with an asterix.

Competition Mechanism	Traits	Mean	SD	Range	n	r	p
Scramble	No. of females within 100 m	2.08	1.71	0 - 6	36	-0.064	0.716
	Home range (ha)	6.13	2.61	1.59 - 11.19	23	0.14	0.523
Reproductive Endurance	Period when testes scrotal (days)	92.1	22.6	20 - 122	36	0.15	0.399
Contest	Weight (g)	357.1	59.5	243.0 - 502.0	36	0.064	0.730
	Body length (mm)	213.8	14.4	182.0 - 236.0	36	-0.075	0.670
Mate choice	Growth rate (g/day)	0.48	0.69	-0.951 - 1.661	30	0.37	0.049*
Sperm competition	No. of males within 100 m	1.11	0.75	0 - 3	36	-0.41	0.013*

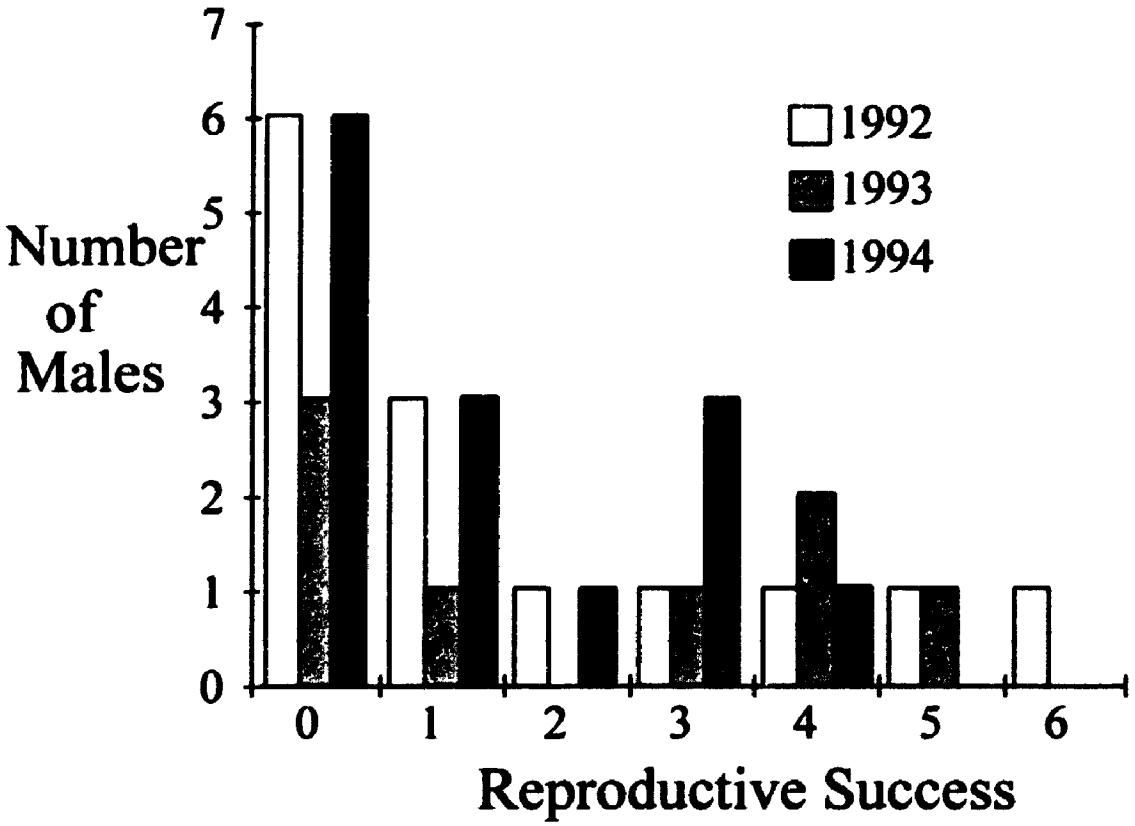

Figure 7. Frequency distribution of reproductive success for all resident males during the period of study (1992 - 94).

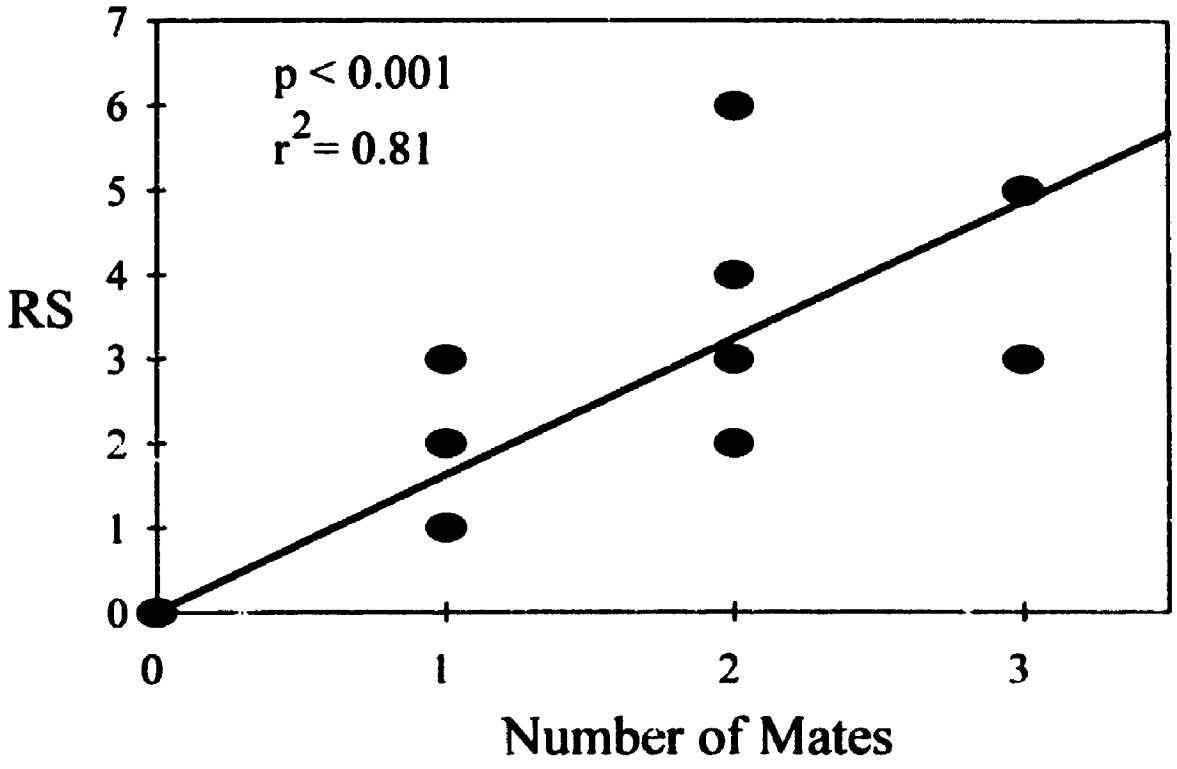

Figure 8. Regression of male reproductive success (RS) and the number of females mated with for each male woodrat for 1992 - 94. (N = 36)

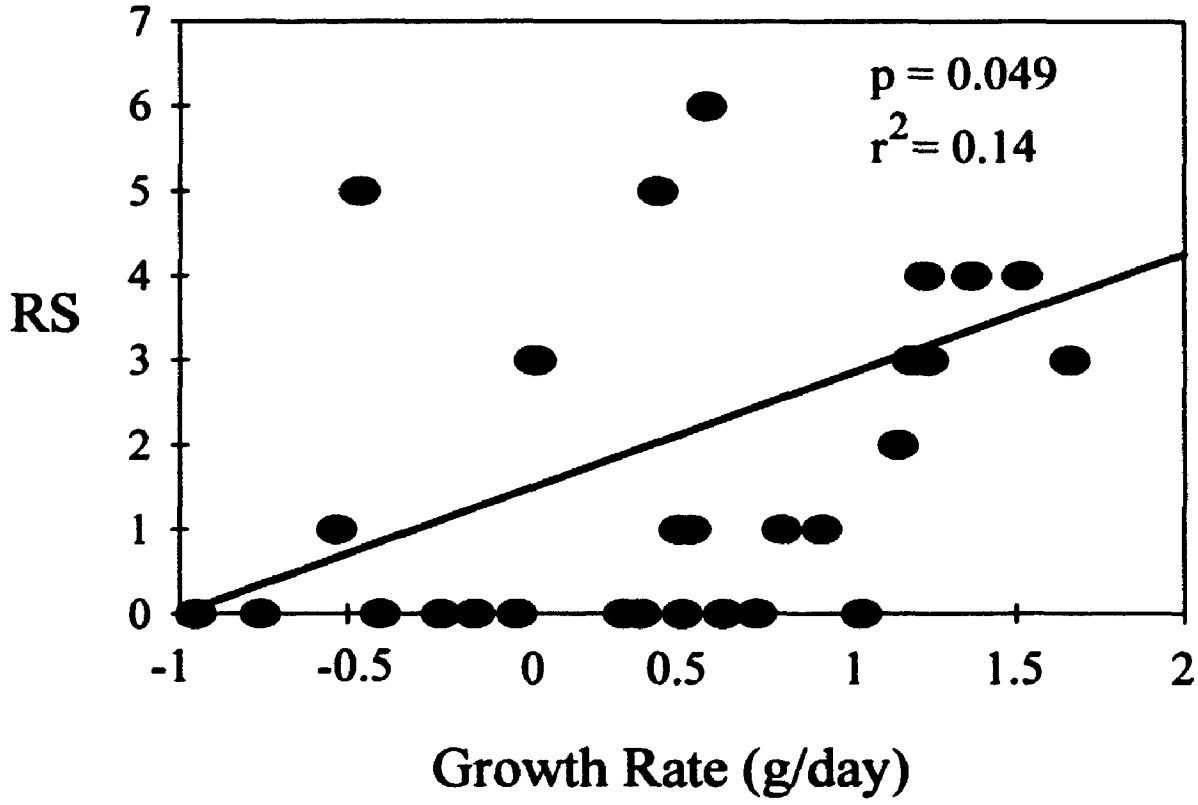

Figure 9. Positive relationship between male growth rate while reproductively active and male reproductive success (RS) for 1992 - 94. (N = 30).

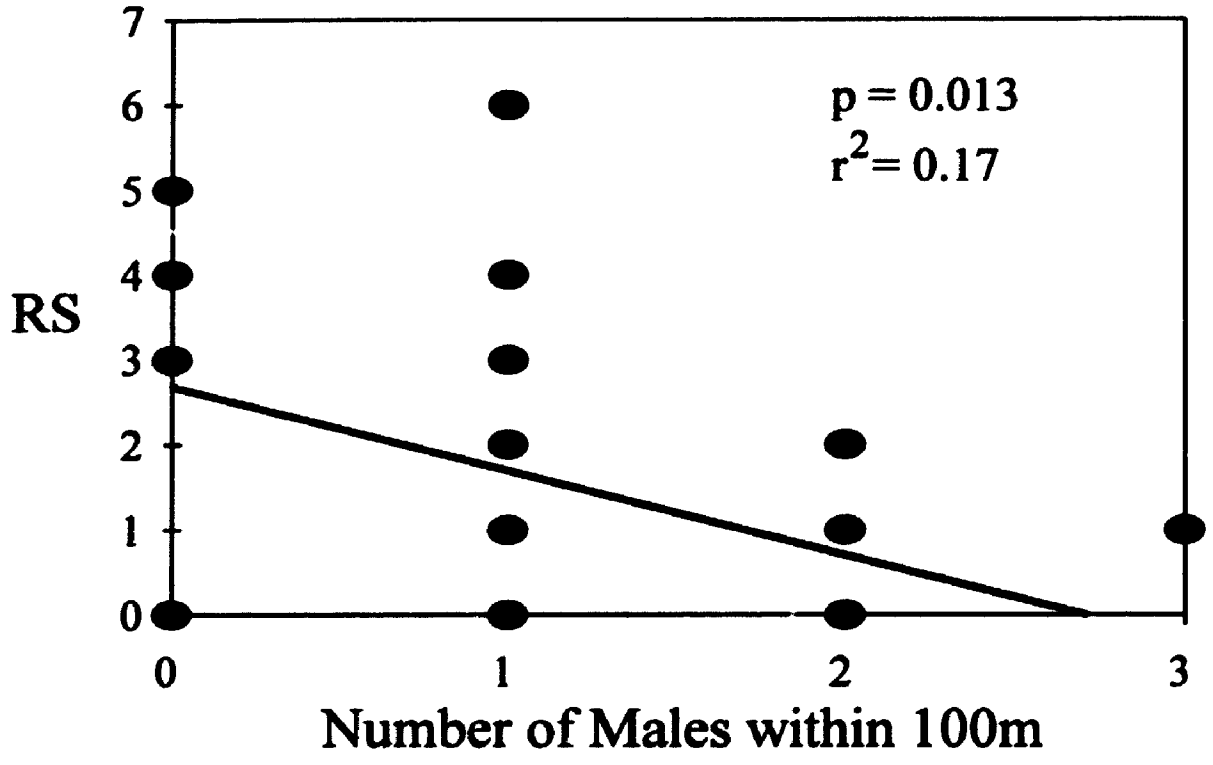

Figure 10. Negative relationship between the number of male nests within 100m of each male nest and male reproductive success (RS) for 1992 - 94. (N = 36).

CHAPTER 6.

GENERAL SUMMARY

The mating system of bushy-tailed woodrats can best be described as a roving male promiscuous system, where males occupy larger home ranges than females, and attempt to gain exclusive access to females during estrus. Once the female is no longer in estrus, and fertilization is presumably successful, males move on in search of other mates.

In terms of the population structure within a single outcrop, males will gain some reproductive success if they are the sole resident. However, if more than one female is resident on the outcrop, a resident male is unable to monopolize mating opportunities within the outcrop, even if he is the only resident male present.

The high environmental potential for polygyny (EPP) previously reported for this species appears to be tempered by two factors. First, female choice may negate the effects of the high EPP, because even if males were capable of sequestering females, or defending an area utilized by females, they may still be denied mating opportunities. The evidence that females appear to use some indicator of male quality as a measure of their suitability as a mate may lead to this high EPP not being recognized. Second, the high EPP breaks down once the spatial distribution in the forest surrounding the outcrops is taken into account. Although female den sites are aggregated on the rocky outcrops, the extended movements of females from their dens, and their subsequently large home ranges lead to a situation in which it is physically impossible for males to restrict access to

more than one female, or to defend the home ranges of more than one female simultaneously. Therefore, once the spatial distribution of females over their entire area of activity is considered, the apparently high EPP observed from consideration of spatial distribution within the outcrop is negated.

Because of the large and relatively unpredictable movements of females, the optimal strategy for males trying to gain access to females is bet-hedging. By maintaining relatively large areas of occupied space (mean = 6.12 ha), males are able to maintain contact with a number of females. Such contact presumably allows the males to determine whether a female is close to estrus or in estrus, most likely from olfactory cues in the urine of the females. If a female is receptive for mating, an individual male will attempt to gain exclusive mating access. If the male is unsuccessful in his attempts to court this particular female, he still has the opportunity to attempt to mate with any of the other females that his home range overlaps with. By maintaining large, overlapping and therefore non-defensible home ranges, males increase their chances of mating with at least one female. The benefit to females is that they have a number of potential mates to choose from once they enter estrus. By selecting a mate based on his quality, and mating only with him during estrus, females ensure that the genetic material that they pass on to their offspring is of high quality.

The disagreement between the findings of this study and previously established theories on the mating system and behaviour of this species warrants some final consideration. As mentioned earlier, the high EPP reported for this species is misleading, as no consideration was made regarding the movements of females in the forest surrounding the outcrops. In addition, with the increasing use of molecular tools to quantify male and

female reproductive success, it is now being realized that the role of females may be of greater importance in many aspects of mating behaviour (Clutton-Brock 1989; Travis et al. 1996). If female choice is a potent force in shaping mating systems, we may have to reconsider some long held classifications of mating behaviour.

LITERATURE CITED

Alcock, J., Jones, C.E., and Buchmann, S.L. 1977. Male mating strategies in the bee *Centris pallida* Fox (Hymenoptera: Anthophoridae). Am. Nat. 111: 145-155.

Anderson, S.S. & Fedak, M.F. 1985. Grey seal males: Energetic and behavioural links between size and sexual success. Anim. Behav. 33: 829-838.

Andersson, M. 1994. Sexual Selection. Princeton University Press, Princeton, New Jersey.

Apollonio, M., Festa-Bianchet, M., and Mari, F. 1989. Correlates of copulatory success in a fallow deer lek. Behav. Ecol. Sociobiol. 25: 89-97.

Armitage, K.B. 1975. Social behavior and population dynamics of marmots. Oikos. 26: 341-354.

Avise, J.C. 1994. Molecular markers, natural history and evolution. Chapman and Hall, New York

Bailey, R.C. 1992. Why we should stop trying to measure the cost of reproduction correctly. Oikos. 65: 349-352.

Bateman, A.J. 1948. Intra-sexual selection in *Drosophila*. Heredity. 2: 349-368.

Bekoff, M., Daniels, T.J., and Gittleman, J.L. 1984. Life history patterns and the comparative social ecology of carnivores. Ann. Rev. Ecol. Syst. 15: 191-232.

Birkhead, T.R., and Møller, A.P. 1992. Sperm Competition in Birds: Evolutionary Causes and Consequences. Academic Press, London.

Birkhead, T.R., and Møller, A.P. 1993. Sexual selection and the temporal separation of reproductive events: sperm storage data from reptiles, birds and mammals. Bio. J. Linn. Soc. 50: 295-311.

Boellstorff, D.E., and Owings, D.H. 1995. Home range, population structure, and spatial organization of California ground squirrels. J. Mamm. 76: 551-561.

Boellstorff, D.E., Owings, D.H., Penedo, M.C.T., and Hersek, M.J. 1994. Reproductive behaviour and multiple paternity of California ground squirrels. Anim. Behav. 47: 1057-1064.

Boonstra, R., Xia, X., and Pavone, L. 1993. Mating system of the meadow vole, *Microtus pennsylvanicus*. Behav. Ecol. 4: 83-89.

Brandt, C.A. 1989. Mate choice and reproductive success of pikas. Anim. Behav. 37: 118-132.

Bronson, F.H., and Marsteller, F.A. 1985. Effect of short-term food deprivation on reproduction in female mice. Biol. Reprod. 33: 660-667.

Brown, J. H. 1968. Adaptation to environmental temperature in two species of woodrats, *Neotoma cinerea* and *N. albigula*. Misc. Publ. Mus. Zool. Univ. Mich. 135: 1-48.

Burke, T., and Bruford, M.W. 1987. DNA fingerprinting in birds. Nature. 327: 149-152.

Burt, W.H. 1943. Territoriality and home range concepts as applied to mammals. J. Mamm. 24: 346-352.

Burt, W.H., and Grossenheider, R.P. 1976. 3rd ed. A field guide to the mammals. Houghton Mifflin Company, Boston.

Cameron. G.N., and Spencer, S.R. 1985. Assessment of space-use patterns in the hispid cotton rat *(Sigmodon hispidus)*. Oecologia 68: 133-139.

Campagna, C. and Le Boeuf, B.J. 1988. Reproductive behaviour of southern sea lions. Behaviour. 104: 233-261.

Cantoni, D., and Vogel, P. 1989. Social organization and mating system of free-ranging, greater white-toothed shrews, *Crocidura russula*. Anim. Behav. 38: 205-214.

Charnov, E.L. 1976. Optimal foraging: the marginal value theorem. Theor. Pop. Biol. 9: 129-136.

Clutton-Brock, T.H. 1988. Reproductive Success. University of Chicago Press, Chicago.

Clutton-Brock, T.H. 1989. Mammalian mating systems. Proc. R. Soc. Lond. B. 236: 339-372.

Clutton-Brock, T.H. 1991. The Evolution of Parental Care. Princeton University Press, New Jersey.

Clutton-Brock, T H., and Parker, G.A. 1992. Potential reproductive rates and the operation of sexual selection. Quart. Rev. Biol. 67: 437-456.

Clutton-Brock, T.H., Albon, S.D., and Guinness, F.E. 1982. Red Deer: Behavior and Ecology of Two Sexes. University of Chicago Press, Chicago.

Clutton-Brock, T.H., Albon, S.D., Gibson, R.M., and Guinness, F.E. 1979. The logical stag: Adaptive aspects of fighting in red deer *(Cervus elephas* L.*)*. Anim. Behav. 27: 211-225.

Clutton-Brock, T.H., Green, D., Hiraiwa-Hasegawa, M., and Albon, S.D. 1988. Passing the buck: resources defense, lekking and mate choice in fallow deer. Behav. Ecol. Sociobiol. 23: 281-296.

Cohen, J.E. 1990. DNA fingerprinting for forensic identification: potential effects on data interpretation of subpopulation heterogeneity and band number variability. Am. J. Hum. Genet. 46: 358-368.

Cranford, J.A. 1977. Home range and habitat utilization by *Neotoma fuscipes* as determined by radiotelemetry. J. Mamm. 58: 165-172.

Darwin, C. 1874. The Descent of Man, and Selection in Relation to Sex. 2nd edition. Murray, London.

Davis, L.S., and Murie, J.O. 1985. Male territoriality and the mating system of Richardson's ground squirrels *(Spermophilus richardsonii)*. J. Mamm. 66: 268-279.

Deutsch, C.J., Haley, M.P., and Le Boeuf, B.J. 1990. Reproductive effort of male northern elephant seals: estimates from weight loss. Can. J. Zool. 68: 2580-2593.

Dixon, K.R., and Chapman, J.A. 1980. Harmonic mean measure of animal activity areas. Ecology. 61: 1040-1044.

Egoscue, H.J. 1962. The bushy-tailed woodrat: a laboratory colony. J. Mamm. 43: 328-337.

Emlen, S.T., and Oring, L.W. 1977. Ecology, sexual selection, and the evolution of mating systems. Science. 197: 215-223.

Endler, J.A. 1986. Natural Selection in the Wild. Princeton University Press, Princeton, New Jersey.

Escherich, P.C. 1981. Social biology of the bushy-tailed woodrat, *Neotoma cinerea*. Univ. Calif. Publ. Zool. 110: 1-132.

Finley, R.B. 1958. The woodrats of Colorado: distribution and ecology. Univ. Kans. Mus. Nat. Hist. Publ. 10: 213-552.

Finley, R. B. 1990. Woodrat Ecology and Behavior and the interpretation of Paleomiddens. *In*: Packrat Middens: the last 40,000 years of

biotic change. *Edited by* J. L. Betancourt, T. R. Van Devender and P. S. Martin. University of Arizona Press, Arizona. pp. 28-42.

Fisher, R.A. 1930. The Genetical Theory of Natural Selection. Clarendon Press, Oxford.

Francis, C.M., Anthony, E.L.P., Brunton, J.A., and Kunz, T.H. 1994. Lactation in male fruit bats. Nature. 367: 691-692.

Frank, S.A. 1990. Sex allocation theory for birds and mammals. Ann. Rev. Ecol. Syst. 21: 13-55.

Gaulin, S.J.C., and Fitzgerald, R.W. 1988. Home-range size as a predictor of mating systems in *Microtus*. J. Mamm. 69: 311-319.

Getz, L.L., and Hofmann, J.E., 1986. Social organization in free-living prairie voles, *Microtus ochrogaster*. Behav. Ecol. Sociobiol. 18: 275-282.

Gomendino, M,, and Roldan, E.R.S. 1993. Mechanisms of sperm competition: linking physiology and behavioural ecology. TREE. 8: 95-100.

Gosling, L.M. 1986. The evolution of mating strategies in male antelope. *In*: Ecological Aspects of Social Evolution. *Edited by* D.I. Rubenstein and R.W. Wrangham. Princeton University Press, Princeton, New Jersey. pp. 244-281.

Gross, M.R. 1985. Disruptive selection for alternative life histories in salmon. Nature. 313: 47-48.

Halliday, T.R. 1983. The study of mate choice. *In*: Mate Choice. *Edited by* P. Bateson. Cambridge University Press, Cambridge. pp. 3-32.

Hamilton, W.D. 1964. The genetical evolution of social behaviour. I, II. J. Theor. Biol. 7: 1-52.

Handford, P., and Mares, M.A. 1985. The mating systems of ratites and tinamous: an evolutionary perspective. Bio. J. Linn. Soc. 25: 77-104.

Harris, S., Cresswell, W.J., Forde, P.G., Trewhella, W.J., Woollard, T., and Wray, S. 1990. Home-range analysis using radio-tracking data-a review of problems and techniques particularly as applied to the study of mammals. Mamm. Rev. 20: 97-123.

Hickling, G.J. 1987. Seasonal reproduction and group dynamics of bushy-tailed woodrats, (*Neotoma cinerea*). Ph.D. thesis, University of Western Ontario, London, Ontario.

Hickling, G.J., Millar, J.S., and Moses, R.A. 1991. Reproduction and nutrient reserves of bushy-tailed woodrats *(Neotoma cinerea)*. Can. J. Zool. 69: 3088-3092.

Hill, W.G. 1986. DNA fingerprint analysis in immigration test-cases. Nature. 322: 290-291.

Hofmann, J.E., Getz, L.L., and Gavish, L. 1984. Home range overlap and nest cohabitation of male and female prairie voles. Am. Midl. Nat. 112: 314-319.

Holmes, W.G. 1984. The ecological basis of monogamy in Alaskan hoary marmots. *In*: The biology of ground dwelling squirrels. *Edited by* J.O. Murie and G.R. Michener. University of Nebraska Press, Lincoln. pp. 250-274.

Howard, R.D. 1978. The evolution of mating strategies in bullfrogs, *Rana catesbeiana*. Evolution. 32: 850-871.

Huck, U.W., Banks, E.M., and Wang, S.-C. 1981. Olfactory discrimination of social status in the brown lemming. Behav. Neur. Bio. 33: 364-371.

Ims, R.A. 1987. Male spacing systems in microtine rodents. Am. Nat. 130: 475-484.

Jeffreys, A.J., Wilson, V., and Thein, S.L. 1985a. Hypervariable 'minisatellite' regions in human DNA. Nature. 314: 67-73.

Jeffreys, A.J., Wilson, V., and Thein, S.L. 1985b. Individual-specific 'fingerprints' of human DNA. Nature. 316: 76-79.

Kenward, R. 1987. Wildlife Radio Tagging: Equipment, Field Techniques and Data Analysis. Academic Press, London.

Kenward R, 1990. RANGES IV. Software for analyzing animal location data. Institute of Terrestrial Ecology, Wareham.

Kitchen, D.W. 1974. Social behavior and ecology of the pronghorn. Wildlife Monographs. 38: 1-96.

Kleiman, D.G. 1977. Monogamy in mammals. Q. Rev. Biol. 52: 39-69.

Kluge, A.G. 1981. The life-history, social organization and parental behavior of *Hyla rosenbergii* Boulenger, a nest-building gladiator frog. Misc. Publ. Mus. Zool. Univ. Mich. 160: 1-170.

Kruuk, H. 1978. Spatial organization and territorial behaviour of the European badger *Meles meles*. J. Zool., Lond. 184: 1-19.

Kruuk, H. 1995. Wild otters: predation and populations. Oxford University Press, Oxford.

Lambin, X., and Krebs, C.J. 1991. Spatial organization and mating system of *Microtus townsendii*. Behav. Ecol. Sociobiol. 28: 353-363.

Lambin, X., Krebs, C.J., and Scott, B. 1992. Spacing system of the tundra vole *(Microtus oeconomus)* during the breeding season in Canada's western Arctic. Can. J. Zool. 70: 2068-2072.

Le Boeuf, B.J. 1974. Male-male competition and reproductive success in elephant seals. Am. Zool. 14: 163-176.

Le Boeuf, B.J., and Reiter, J. 1988. Lifetime reproductive success in northern elephant seals. *In*: Reproductive Success. *Edited by* T.H. Clutton-Brock. University of Chicago Press, Chicago. pp. 344-362.

MacKinnon, J.R. 1974. The ecology and behaviour of wild orang-utans *(Pongo pygmaeus)*. Anim. Behav. 22: 3-74.

Madison, D.M. 1980. Space use and social structure in meadow voles, *Microtus pennsylvanicus*. Behav. Ecol. Sociobiol. 7: 65-71.

Maniatis, T., Fritsch, E.F., and Sambrook, J. 1982. Molecular cloning: a laboratory approach. Cold Spring Harbor Laboratories, New York.

Marinelli, L., Messier, F. and Plante, Y. 1992. Use of DNA fingerprinting to determine parentage in muskrats *(Ondatra zibethicus)*. J. Hered. 83: 356-360.

McRae, S.B., and Kovacs, K.M. 1994. Paternity exclusion by DNA fingerprinting, and mate guarding in the hooded seal *Cystophora cristata*. Mol. Ecol. 3: 101-107.

Merson, M.H., and Kirkpatrick, R.L. 1983. Role of energy intake in the maintenance of reproduction in female white-footed mice. Am. Midl. Nat. 109: 206-208.

Millar, C.D., Anthony, I., Lambert, D.M., Stapleton, P.M., Bergmann, C.C., Bellamy, A.R., and Young, E.C. 1994. Patterns of reproductive success determined by DNA fingerprinting in a communally breeding oceanic bird. Bio. J. Linn. Soc. 52: 31-48.

Millar, J.S. 1977. Adaptive features of mammalian reproduction. Evolution. 31: 370-386.

Moses, R.A. 1992. Intrasexual competition and reproductive success in female bushy-tailed woodrats. Ph.D. thesis, University of Western Ontario, London, Ontario.

Moses, R.A., and Millar, J.S. 1992. Behavioural asymmetries and cohesive mother-offspring sociality in bushy-tailed woodrats. Can. J. Zool. 70: 597-604.

Moses, R.A., and Millar, J.S. 1994. Philopatry and mother-daughter associations in bushy-tailed woodrats: space use and reproductive success. Behav. Ecol. Sociobiol. 35: 131-140.

Nishida, T. and Hiraiwa-Hasegawa, M. 1987. Chimpanzees and bonobos: cooperative relationships among males. *In*: Primate societies. *Edited by* B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham, and T.T. Struhsaker. University of Chicago Press, Chicago. pp. 165-178.

Ogilvie, R.T. 1969. The mountain forest and alpine zones of Alberta. *In*: Vegetation, soils and wildlife. *Edited by* J.C. Nelson and M.J. Chambers. Methuen Publishing, Toronto. pp. 24-44.

Olds, N., and Shoshani, J. 1982. *Procavia capensis*. Mamm. Spec. 171: 1-7.

Orians, G.H. 1969. On the evolution of mating systems in birds and mammals. Am. Nat. 103: 589-603.

Ostfeld, R.S. 1985. Limiting resources and territoriality in microtine rodents. Am. Nat. 126: 1-15.

Ostfeld, R.S. 1986. Territoriality and mating system of California voles. J. Anim. Ecol. 55: 691-706.

Ostfeld, R.S., Lidicker, W.Z., and Heske, E.J. 1985. The relationship between habitat heterogeneity, space use, and demography in a population of California voles. Oikos. 45: 433-442.

Ostfeld, R.S., Pugh, S.R., Seamon, J.O., and Tamarin, R.H. 1988. Space use and reproductive success in a population of meadow voles. J. Anim. Ecol. 57: 385-394.

Parker, G.A. 1970. Sperm competition and its evolutionary consequences in the insects. Biol. Rev. 45: 525-567.

Parker, G.A. 1984. Sperm competition and the evolution of mating strategies. *In*: Sperm competition and the evolution of animal mating systems. *Edited by* R.L. Smith. Academic Press, London. pp. 1-60.

Parker, G.A., Simmons, L.W., and Kirk, H. 1990. Analysing sperm competition data: simple models for predicting mechanisms. Behav. Ecol. Sociobiol. 27: 55-65.

Peterson, R.L. 1955. North American moose. University of Toronto Press, Toronto

Pierce, J.D., Ferguson, B., Salo, A.L., Sawrey, D.K., Shapiro, L.E., Taylor, S.A., and Dewsbury, D.A. 1990. Patterns of sperm allocation across successive ejaculates in four species of voles *(Microtus)*. J. Reprod. Fert. 88: 141-149.

Queller, D.C., Strassmann, J.E., and Hughes, C.R. 1993. Microsatellites and kinship. TREE. 8: 285-288.

Ramsay, M.A., and Stirling, I. 1986. On the mating system of polar bears. Can. J. Zool. 64: 2142-2151.

Randall, J.A. 1991. Mating strategies of a nocturnal, desert rodent *(Dipodomys spectabilis)*. Behav. Ecol. Sociobiol. 28: 215-220.

Ribble, D.O. 1991. The monogamous mating system of *Peromyscus californicus* as revealed by DNA fingerprinting. Behav. Ecol. Sociobiol. 29: 161-166.

Ribble, D.O. 1992. Lifetime reproductive success and its correlates in the monogamous rodent, *Peromyscus californicus*. J. Anim. Ecol. 61: 457-468.

Ribble, D.O., Millar, J.S. in press. The mating system of northern populations of *Peromyscus maniculatus* as revealed by radiotelemetry and DNA fingerprinting. Ecoscience.

Ribble, D.O., and Salvioni, M. 1990. Social organization and nest co-occupancy in *Peromyscus californicus*, a monogamous rodent. Behav. Ecol. Sociobiol. 26: 9-15.

Ridley, M. 1978. Paternal care. Anim. Behav. 26: 904-932.

Ridley, M. 1983. The Explanation of Organic Diversity: The Comparative Method and Adaptations for Mating. Clarendon, Oxford.

Rood, J.P. Ecology and social evolution in the mongooses. *In*: Ecological aspects of social evolution. *Edited by* D.I. Rubenstein and R.W. Wrangham. Princeton University Press, Princeton, New Jersey. pp. 131-152.

Ryser, J. 1992. The mating system and male mating success of the Virginia opossum *(Didelphis virginiana)* in Florida. J. Zool., Lond. 228: 127-139.

Salvioni, M. 1988. Home range and social behavior of three species of European *Pitymys* (Mammalia: Rodentia). Behav. Ecol. Sociobiol. 22: 203-210.

Schaller, G.B. 1971. The Serengeti Lion. Chicago University Press, Chicago.

Schwagmeyer, P.L. 1988. Scramble-competition polygyny in an asocial mammal: male mobility and mating success. Am. Nat. 131: 885-892.

Schwagmeyer, P.L., and Brown, C.H. 1983. Factors affecting male-male competition in thirteen-lined ground squirrels. Behav. Ecol. Sociobiol. 13: 1-6.

Schwagmeyer, P.L., and Woontner, S.J. 1986. Scramble competition polygyny in thirteen-lined ground squirrels: The relative contributions of overt conflict and competitive mate searching. Behav. Ecol. Sociobiol. 19: 359-364.

Shapiro, L.E., and Dewsbury, D.A. 1986. Male dominance, female choice and male copulatory behavior in two species of voles *(Microtus ochrogaster* and *Microtus montanus)*. Behav. Ecol. Sociobiol. 18: 267-274.

Shields, W.M. 1987. Dispersal and mating systems: Investigating their causal connections. *In*: Mammalian Dispersal Patterns. *Edited by* B.D. Chepko-Sade and Z. T. Halpin. University of Chicago Press, Chicago. pp. 3-26.

Solomon, N.G. 1993. Body size and social preferences of male and female prairie voles, Microtus ochrogaster. Anim. Behav. 45: 1031-1033.

Southern, E. 1975. Detection of specific sequences among DNA fragments separated by gel electrophoresis. J. Mol. Biol. 98: 503-517.

Southwood, T.R.E. 1966. Ecological Methods: with Particular Reference to the Study of Insect Populations. Chapman and Hall, London.

Stockley, P., Searle, J.B., Macdonald, D.W., and Jones, C.S. 1994. Alternative reproductive tactics in male common shrews: relationships between mate-searching behaviour, sperm production, and reproductive success as revealed by DNA fingerprinting. Behav. Ecol. Sociobiol. 34: 71-78.

Svensson, I. 1988. Reproductive costs in two sex-role reversed pipefish species *(Syngnathidae)*. J. Anim. Ecol. 57: 929-942.

Swihart, R.K., and Slade, N.A. 1985. Testing for independence of observations in animal movements. Ecology. 66: 1176-1184.

Tamarin, R.H., Sheridan M., and Levy, C.K. 1983. Determining matrilineal kinship in natural populations of rodents using radionuclides. Can. J. Zool. 61: 271-274.

Tegelstrom, H., Searle, J., Brookfield, J., and Mercer, S. 1991. Multiple paternity in wild common shrews *(Sorex araneus)* is confirmed by DNA-fingerprinting. Hereditary. 66: 373-379.

Thorne, H.V. 1967. Electrophoretic characterization and fractionation of polyoma virus DNA. J. Mol. Biol. 24: 203.

Travis, S.E, Slobodchikoff, C.N., and Keim, P. 1996. Social assemblages and mating relationships in prairie dogs: a DNA fingerprint analysis. Behav. Ecol. 7: 95-100.

Trillmich, F. 1986. Are endotherms emancipated? Some considerations on the cost of reproduction. Oecologia. 69: 631-633.

Trivers, R.L. 1972. Parental investment and sexual selection. *In*: Sexual Selection and the Descent of Man, 1871-1971. *Edited by* B. Campbell. Heinemann, London. pp. 136-179.

Van Winkle, W. 1975. Comparisons of several probabilistic home-range models. J. Wildl. Man. 39: 118-123.

Vaughan, T. A. 1990. Ecology of Living Packrats. *In*: Packrat Middens: the last 40,000 years of biotic change. *Edited by* J. L. Betancourt, T. R. Van Devender and P. S. Martin. University of Arizona Press, Arizona. pp. 14-27.

Verner, J., and Willson, M.F. 1966. The influence of habitats on mating systems of North American passerine birds. Ecology. 47: 143-147.

Westneat, D.F. 1990. Genetic parentage in the indigo bunting: a study using DNA fingerprinting. Behav. Ecol. Sociobiol. 27: 67-76.

Wickings, E.J., Bossi, T., and Dixson, A.F. 1993. Reproductive success in the mandrill, *Mandrillus sphinx*: correlations of male dominance and mating success with paternity, as determined by DNA fingerprinting. J. Zool., Lond. 231: 563-574.

Williams, G.C. 1966. Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought. Princeton University Press, Princeton, New Jersey.

Wittenberger, J.F. 1979. The Evolution of mating systems in birds and mammals. *In*: Handbook of Behavioral Neurobiology. 3. Social behavior and communication. *Edited by* P. Marler and J.G. Vandenbergh. Plenum Press, New York. pp. 271-349.

Wolff, J.O. 1993. Why are female small mammals territorial ? Oikos 68: 364-370.

Wootton, R.J. 1984. A functional Biology of Sticklebacks. Croom Helm, London.

Xia, X., and Millar, J.S. 1991. Genetic evidence of promiscuity in *Peromyscus leucopus*. Behav. Ecol. Sociobiol. 28: 171-178.

Zar, J.H. 1984. Biostatistical analysis, 2nd edition. Prentice-Hall, New Jersey.